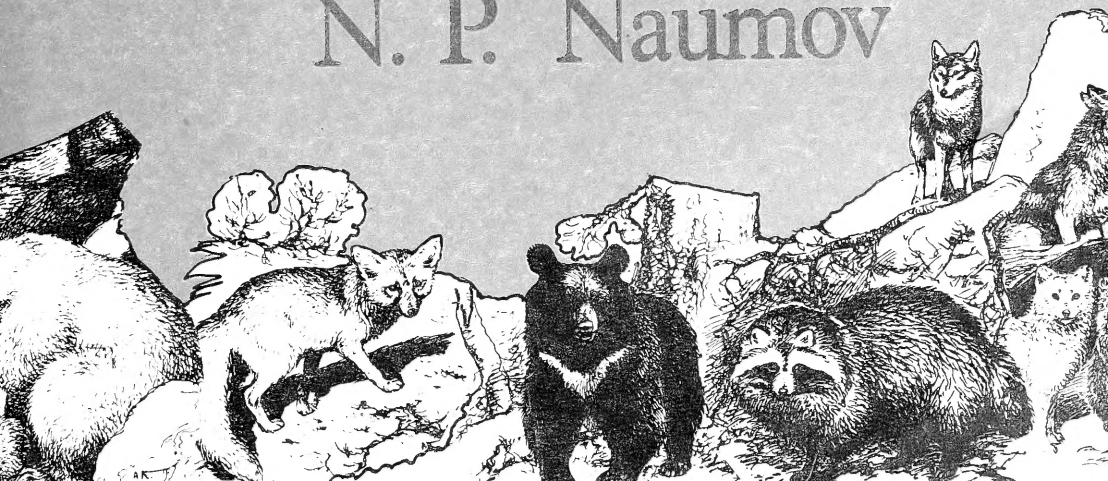


Mammals of the Soviet Union

VOLUME II Part 1a

V. G. Heptner

N. P. Naumov



The present book, of the series *Mammals of the Soviet Union, Sirenia and Carnivora*, is the fourth volume to be published in English. Previously Volume I — *Artiodactyla and Perissodactyla*, Volume II, part 2 — *Carnivora (Hyenas and Cats)* and Volume II, part 3 — *Pinnipeds and Toothed Whales* were published in 1988, 1992, and 1996 respectively. *Sea Cows, Wolves and Bears* constituted the second in the series to appear.

The original Russian book is so large (982 pp.) that its publication in the English translation format would have resulted in a book of about 1400 pages, which was considered too unwieldy. Therefore, it was decided to publish Volume II, Part 1 — *Sirenia and Carnivora*, in two roughly equal parts. The first (Part 1a) consists of the Steller's sea cow, the now-extinct marine mammal once found only around the Commander Islands in the western Bering Sea, and the Russian species of the wolf and bear families. The second half (Part 1b) will comprise the various members of the weasel family, plus the introduced American raccoon. As indicated in the foreword to the English edition of Volume I, the senior author and editor of the series, Dr. Vladimir Georgievich Heptner, died in 1975, and did not complete the projected series. However, work continues, and Russian volumes on baleen whales, lagomorphs and dipodid rodents are now published.

A final point: since the appearance of Volume II, part 2, the Soviet Union has disappeared. However, the series was written in the context of the former "union of republics," and it would be confusing to re-edit the text to conform to the current political reality.

Mammals of the Soviet Union

Volume II

Part 1a

MAMMALS OF THE SOVIET UNION

In Three Volumes

Edited by

V.G. Heptner and N.P. Naumov

Vysshaya Shkola Publishers
Moscow, 1967

Mammals of the Soviet Union

Volume II, Part 1a

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(Sea Cows; Wolves and Bears)

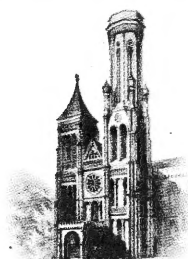
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Mlekopitayushchie Sovetskogo Soyuz

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Foreword to the English Edition

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

The present book of the series *Mammals of the Soviet Union, Sirenia and Carnivora*, is the fourth volume to be published in English. The project was initiated in 1975 as my contribution to joint U.S. – U.S.S.R. studies on Holarctic mammals, sponsored by the Environmental Agreement between the two countries. Previously, Volume I, *Artiodactyla and Perissodactyla*, Volume II, part 2, *Carnivora (Hyenas and Cats)* and Volume II, part 3, *Pinnipeds and Toothed Whales* were published in 1988, 1992, and 1996 respectively.

Sea Cows, Wolves and Bears constituted the second in the series to appear. The fact that this volume was not published in English translation in the proper sequence is due to the fact that the translation was performed under a different contract from that supervised by Amerind Publishing Company, New Delhi, India. Moreover, the original Russian book is so large (982 pp.) that its publication in the English translation format would have resulted in a book of about 1400 pages, which we considered too unwieldy. Therefore, it was decided to publish Volume II, Part 1, *Sirenia and Carnivora*, in two roughly equal parts. The first (Part 1a) consists of the Steller's sea cow, the now-extinct marine mammal once found only around the Commander Islands in the western Bering Sea, and the Russian species of the wolf and bear families. The second half (Part 1b) will comprise the various members of the weasel family, plus the introduced American raccoon.

As indicated in the foreword to the English edition of Volume I, the senior author and editor of the series, Dr. Vladimir Georgievich

Heptner, died in 1975, and did not complete the projected series. However, work continues, and Russian volumes on baleen whales, lagomorphs and dipodid rodents are now published. It is hoped that English translations of these later volumes will follow more promptly than has been true of the first volumes of the series.

English readers interested in Dr. Heptner's contributions as a mammalogist should refer to the foreword to the English edition of Volume I. Conventions used in rendering geographic names, first stated there, are reprinted here for the convenience of the reader. Geographic names are generally transliterated directly, but a few exceptions were permitted (e.g. Moscow instead of Moskva, translation rather than transliteration of certain modifiers of place names, such as Northern, rather than Severnaya, Dvina). Soviet administrative units are numerous, and the following equivalents were employed in translation: *krai*, territory; *oblast'*, district; *raion*, region; *guberniya* (archaic), governance, *uyezd*, county. Also, in the original Russian text, rivers, mountain ranges, and cities are often not explicitly identified, the Soviet reader being presumed sufficiently familiar with the geography of the country to be able to understand from the context of the sentence what sort of place is referred to. Complicating the matter is the lack of articles as parts of speech in Russian. To assist the English reader, I have adopted the following conventions: if a river is referred to, an article precedes it; if a mountain range is referred to, it is translated as a plural; if a city is referred to, it is singular, and lacks the article. Examples are: the Ural (river); the Urals (mountains); Ural'sk (city). Geographic place names are also inflected in Russian, and these have been simplified by omitting transliteration of the inflected ending. For example, the Russian phrase *v Yaroslavskoi i Kostromskoi oblastiakh* is translated "in the Yaroslavl and Kostroma districts." In cases where the nominative form of the place name has an -sk ending this is, however, transliterated (e.g., Omsk); when a Russian "soft sign" is employed in a place name, this is transliterated as an apostrophe (e.g. Khar'kov); the "hard sign" is rendered as a double apostrophe. Because of the large number of place names in this volume, it was not possible to verify all of them, and some inconsistencies are likely to occur. I would appreciate it if readers would bring any errors they may notice to my attention.

In Volume II, part 1, I have also attempted to improve certain aspects of the translation in order to reflect more faithfully the original Russian text. For example, what was translated as "taxonomy" in

volume I is now in some places rendered as “systematic position;” what was “economic importance” is now “practical significance,” etc.

One further point of confusion not apparent to me when Volume I was translated also required clarification; that is the English transliteration of the senior author’s surname. This begins with the fourth letter of the Cyrillic alphabet, which usually has a “G” sound in Russian. However, the surname was originally German (as indeed was mine) and in the original German began with the letter “H” of the Latin alphabet. Since Cyrillic has no equivalent of “H” this is usually transliterated into “G” in Russian. However, I know from conversations with him that Dr. Heptner preferred to use the original Germanic form of his surname rather than the transliterated version, which is rendered as Geptner. The rules of transliteration employed by the Library of Congress do not permit such flexibility, and the attentive reader may notice that Library of Congress cataloging employs the latter.

A final point: since the appearance of Volume II, part 2, the Soviet Union has disappeared. However, the series was written in the context of that former “union of republics,” and it would be confusing to re-edit the text to conform to the current political reality.

Robert S. Hoffmann
National Museum of Natural History
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Washington, D.C.

Foreword

- 5 The second volume of the "Mammals of the Soviet Union" is devoted to descriptions of the terrestrial Carnivores (Order Carnivora), and the sea cows (Order Sirenia), consisting in our fauna of only one recently extinct species. There is a great deal of information in our country about carnivorous mammals, which include the most important fur animals. In the last 10 years they [furbearers] have been studied in especially great detail. Various unpublished data of importance available to the authors were included in the descriptions. Therefore, the size of this book is considerable.

All species in the indigenous families of the Order Carnivora are described with the exception of the cats (Felidae) and hyaenas (Hyaenidae), i.e. the suborder Feloidae. Descriptions of these excluded families will follow in the next volume. In addition, the book includes two acclimatized American species of carnivores—raccoon and mink. The striped skunk, as is known, failed to be acclimatized in our country and is therefore not included.

The classification of this order follows Simpson (1945). Simpson's orders themselves are, as is known, conventional. Only one exception is admitted: pinnipeds, contrary to the opinion of Simpson and some others, are considered as an independent order. The arrangement of orders in the book follows the sequence from most specialized to the most primitive, that is to say, from up to down. Within the orders in this volume—as in volume I—the taxa and species are arranged, according to their specialization. In the sequence of orders described, however, one other deviation was made: carnivores (Carnivora), and not pinnipeds (Pinnipedia) were placed after the sea cows, in order that pinnipeds and whales could be included in one volume. For orientation to the actual relationships of orders, a macrosystemic scheme of the class is given [pg. xix].

All the characteristics of a group are presented in a standard format and deviation was permitted in only a few special cases. Group characteristics, given in an extremely condensed form, are applicable

not only to the species of our fauna but to the entire group. Principal attention is paid to the distribution and systematic composition of groups, and the phylogenetic relationships of our forms within the group. Paleontological information is very condensed, mainly according to Simpson (1945), but partly from Thenius and Hofer (1960), "Fundamentals of Paleontology" edited by Yu.A. Orlov (1962), and various other sources.

In the species descriptions, attention was mainly concentrated on geographic distribution and biology. Ranges are broadly presented, based on available data, and only limits are described. Habitats within these ranges are not mentioned, and only the most important marginal localities are given. Historical changes in geographic ranges are traced, and as much as possible the description is based on the "reconstructed" range of the species, in depth for centuries of "historical" time. This is, therefore, a suitable opportunity to establish a more or less actual geographic area. A knowledge of this is obligatory for solving theoretical questions of zoogeography and for practical work with the fauna¹.

Ranges beyond the boundaries of our country—including those "reconstructed"—follow numerous works, but chiefly for critical verification, information provided by Seton-Thompson (1909–1910), Miller (1912), Sowerby (1923), Anthony (1928), Aharoni (1930), Nezabitowski (1934), Shortridge (1934), Phillips (1935), Heim-de-Balsac (1936), Allen (1938–1940, 1939, 1942), Pocock (1939, 1941), Cabrera and Yepes (1940), Hamilton (1943), Harper (1945), Simpson (1945), Anderson (1946), Carter, Hill and Tate (1946), Prater (1947), Tate (1947), Troughton (1948), Enar (1949)*, Calinescu (1951), Roberts (1951), Ellerman and Morrison-Scott (1951), Morrison-Scott and Hayman (1953), Bannikov (1954), Laurie and Hill (1954), Miller and Kellog (1955), Siivonen (1956), Haltenorth and Trense (1956) Cabrera (1958, 1960), Van den Brink (1958), Frechkop (1958), Markov (1959), Misonne (1959), Hall and Kelson (1959), Hatt (1959), Dulic and Tortric (1960), Burt and Grossenheider (1962), Burton (1962), Cockrum (1962) and many others. Individual references to the above-mentioned authors were not given in the text descriptions of ranges external to the boundaries of the USSR. North American ranges were based in nearly

¹ More detailed information about reconstructed geographic ranges is available in the work of V.G. Heptner. Dynamics of geographic ranges of some ungulates and human factors. Sb. "Geographical Questions", 1959. [Dinamika areala nekotorykh kopytnykh i antropicheskii faktor. Sb. "Voprosy Geographii," 1959.]

* Not in Lit. Cit.—Sci. Ed.

all cases on excellent maps in Hall and Kelson (1959), whose opinions differed completely, in some cases, from the description of others. All maps of geographic ranges are original, prepared by V.G. Heptner.

Unfortunately, we have not succeeded in achieving uniformity among different authors in describing the biology of species. However, the general format is identical to that encountered in the first volume; only the description of the extinct species—the sea cow—differs. Concerning the latter, instead of paraphrasing the data from published literature, a special translation was made of the original work of Steller—the only naturalist to have observed this animal and studied its anatomy. Until now, *i.e.* for more than 200 years, Steller's text has not appeared in Russian. S. Krasheninnikov (1786), who had Steller's manuscripts, published a translation of only certain parts of this work. Owing to the language in which the work of Steller was published (Latin and old German of the early 18th century), this material was not accessible to most zoologists, as a result of which some disagreements arose in our day. Knowledge and iconography of the species was poor.*

The morphological characteristics of the species have been presented in completely identical, though short, form as far as sufficiently detailed descriptions of the series of taxa and forms. Geographic variation of species within the USSR has, with few exceptions, been revised or critically reevaluated. Variation in those parts of geographic ranges lying beyond the boundaries of the USSR follow the most recent available data, but were not critically reviewed; the described forms are listed and general notes provided.

All synonymys are re-examined and given in an extremely limited scope according to the following principles: only species synonyms are included. Generic synonyms are mentioned only if the type of the genus is a species represented in our fauna, or if the generic reference has significance in that it sometimes has been applied (or previously applied), or may be applied to our species. All references are included in species synonyms in the following cases: 1) if the name was applied to a specimen of a species in our territories; 2) if the name was applied to a specimen of a species taken elsewhere, but is significant
7 in that it is applied or has been applied but is now used for a Soviet form; 3) if the name was given to a specimen from another territory and not applied to our form, but may have significance for some

* Steller's text is now known to be inaccurate in certain respects — Sci. Ed.

Soviet forms; 4) the names applied to type species are always presented regardless of their type locality within or outside of the USSR. Actual names in the species synonymies are not allotted, but are placed in the accounts of subspecies inhabiting our country, and synonymies are also given in relation to the particular subspecies. Synonymies of subspecies distributed outside the USSR are not given. Synonymies of categories above the genus are not mentioned, nor are references to the descriptions and names of these higher orders which, if not stated otherwise, are given by Simpson (1945).

Names applied to domestic forms, following the rationale and usage of the first volume, are not used for wild species; rather the name assigned the wild taxon is employed for the species as a whole.

The total number of mammalian species approximates 3500, and the number of species of our fauna is about 300 (Heptner, 1956).

Each author's contribution in the compilation of this volume was as follows: V.G. Heptner wrote all the general characters of the major taxa (order, family, genus), the entire sections concerning the sea cow (including translation of Steller's text) and the Afghan fox, and all tabular material. He worked out the synonymy of all species and also wrote the sections dealing with the "Description", "Systematic Position", "Geographic Distribution", and "Geographic Variation" for all species described in this volume, and also prepared all maps of geographic range presented in the volume. P.R. Yurgenson wrote the section on "Biology" and "Practical Significance" for the three species of bears, all species of the mustelid family, and the American raccoon. A.A. Sludskii wrote the same sections concerning the corsac fox, jackal and red wolf [dhole] whereas the section on "Biology" and "Practical Significance" for red fox and arctic fox were contributed by A.F. Chirkova; N.P. Naumov wrote the same sections for the gray wolf, and A.G. Bannikov, for the Ussuri raccoon (raccoon dog). Authorship of the separate parts is indicated by bracketed initials at the end of the corresponding sections. Integration of the [above] system, species arrangement, their limits, number and limits of subspecies as well as all the synonymies are the responsibility of V.G. Heptner.

The literature up to the period 1961–1962 was more or less completely employed. Some works which appeared after that period were not referred to, especially the information provided by I.M. Gromov, A.A. Gureev, G.A. Novikov, I.I. Sokolov, P.P. Strelkov, and K.K. Chapskii ("Mammal fauna of USSR" 1963). We have succeeded in only individual cases in making use of data from papers published

after this period. Literature references are usually given parenthetically by surname and year, initials being given only when more than one author has the same surname. References to author's unpublished data, personal communications, or letters are given without reference to year, but the author's initials are given to distinguish them from published citations.

The authors have, of course, included their unpublished personal observations in this work, and this is sometimes referred to as noted above. In addition much unpublished material of different types was kindly supplied to the authors by G.F. Bromlei (Vladivostok), N.K. Vereshchagin (Leningrad), N.N. Vorontsov (Moscow), S.V. Kirikov (Moscow), V.V. Kozlov (Krasnoyarsk), A.P. Korneev (Kiev), V.P. Kostin (Tashkent), B.A. Kuznetsov (Moscow), N.I. Larina (Saratov) Kh. I. Ling (Tartu), R.N. Meklenburtsev (Tashkent), L.G. Morozova - Turova (Moscow), V.N. Nadeev (Irkutsk), T.A. Pavlenko (Tashkent), V.Ya. Parovshchikov (deceased) (Arkhangel'sk), V.N. Pavlinin (Sverdlovsk) V.A. Popov (Kazakh), S.K. Priklonskii (Oka preserve), R. Rausch (USA), C. Repenning (USA), N.N. Rukovskii (Moscow), N.V. Rakov (Saransk), V.E. Sokolov (Moscow), V.N. Skalon (Alma-
8 Ata), S.U. Stroganov (deceased) (Novosibirsk), N.D. Sysoev (Vladimir), K.A. Tatarinov (L'vov), V.P. Teplov (deceased) (Oka preserve), V.V. Timofeev (Irkutsk), S.M. Uspenskii (Moscow), A.V. Fedoseev (Bryansk), K.K. Chapskii (Leningrad), V.D. Shamykin (Moscow), E.I. Shereshevskii (Moscow), E.I. Shcherbina (Ashkhabad), as well as additional authors especially mentioned in the text.

Useful information concerning the distribution of the different species was also kindly supplied by workers of all the district hunting inspection centers. These were Starodubchenko (Kiev), Lebedev (Volgograd), Mikhailov (Saratov), Zakharov (Murmansk), Gusev (Rostov-on-Don), Khmelevskii (Orenburg), Sukhikh (Belgorod), Ivanov (Yakutsk), Kuz'min and Fofanov (Novosibirsk), Bel'skii (Vladivostok), Anashkin (Ulan-Ude), Samsonov (Blagoveshchensk), and Sysoev (Khabarovsk).

Figures for this volume were assembled by V.G. Heptner. Animal illustrations were prepared by our famous "animalists", A.N. Komarov and N.N. Kondakov. Line drawing of all of the animal species described as well as five of the color plates, were made by A.N. Komarov. Three plates—weasel, red fox and sea cow were done by N.N. Kondakov. The painting of the Steller's cow is considered a trial reconstruction of the species—a collaboration between N.N. Kondakov and V.G. Heptner. The drawing of tracks were, with few exceptions,

taken from Prof. A. N. Formozov's books based on his original sketches from nature.

The skull drawings were done by V.N. Lyakhov based on materials in the Zoological Institute of the Academy of Science, under the supervision of Prof. G.A. Novikov, and were previously published in his book (1956). The original drawings are in the possession of the Zoological Institute of the Academy of Science; thanks to the courtesy of Prof. O.A. Skarlato and Prof. A.A. Strelkov, the Institute has granted permission for their use in this book.

Photographs and other illustrations related to the biological sections of the volume were contributed by various persons, but were mainly taken from the archive of Prof. V.G. Heptner (especially those of mustelid and bear families). A significant portion was provided by A.A. Sludskii (Alma-Ata), Yu.K. Gorelov (Badkhyz preserve), S.V. Marakov (Kirov) and A.G. Pankrat'ev ("Kedrovaya pad" preserve). Those supplying other photographs are cited at appropriate places. All photographs are original, and published here for the first time. Colleagues V.N. Orlov and I.P. Mitina of the Department of Vertebrate Zoology at Moscow State University provided great assistance during the preparation of this book.

We here once more acknowledge with thanks all the above-mentioned persons, organizations and others who helped in the production of this book. The authors especially acknowledge Prof. V.A. Popov (Kazan') and Prof. N.I. Larina (Saratov) who provided great help in the preparation and reading of the manuscript, and who made many useful suggestions.

All work was to a great extent accomplished in the Zoological Museum, Moscow State University, whose rich collections were used. The authors express their gratitude to prior and present directors of this Museum: Professors S.G. Soin and N.A. Gladkov.

The first volume "Mammals of the Soviet Union" was received in our country, and in other countries as well, with great appreciation and was officially and unofficially reviewed and put out in German translation. The authors hope that this volume will also be acceptable, even though they are quite sure that their work is not free from specific and general errors. The authors kindly request those who use their book to inform them of any errors noticed and to send necessary corrections to the following: Professor Vladimir Georgevich Heptner, Zoological Museum, Moscow State University, Herzen St., No. 6, Moscow K-9 [U.S.S.R.].

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*Pages 1000–1001 in Russian original. The English table of contents is not a literal translation.

**Palmer, 1895 in Russian original — Sci. Ed.

***Fisher, 1817 is now considered to have priority — Sci. Ed.

****1843 in Russian original—Sci. Ed.

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*Frisch, 1775 is now considered to have priority — Sci. Ed.

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*Dawkins, 1868 is now considered to have priority — Sci. Ed.

**Fischer, 1817 is now considered to have priority — Sci. Ed.

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† LITERATURE CITED

† INDEX OF LATIN NAMES OF TAXA**

*1774 in Russian original — Sci. Ed.

**The Russian original also included an Index of Russian Names of Taxa, omitted here—Sci Ed.

† These Sections appear at the end of part 1b.—Gen. Ed.

Systematics of the Class Mammalia

- 9 The classification of major subdivisions (orders) adopted in the present publication is based on the systematic monograph of the class by Simpson (1945), who relied extensively on paleontological data. It is very close to the system of classification proposed by M. Weber (1928), which in its time was well founded on the anatomy of extant forms. The orders proposed by Simpson have long been widely recognized and their grouping into higher taxa raises no serious objections.

Extreme division of the orders is a recent trend. Thus, marsupials have been divided into three orders — polyprotodontids-Polyprotodontidia, caenolestids—Caenolestia, and diprotodontids-Diprotodontia, cetaceans into two (toothless whales—Mystacoceti and toothed whales—Odontoceti), primates into three (lemurs—Prosimiae, simians—Simiae, and tarsiers—Tarsioidea), and so on. All these proposals, however, are not yet well founded. Moreover, among mammalian systematists extreme division is not generally favored. Neither is it commended here. An order should be primarily an integrating and not a divisive concept. Otherwise the same situation will arise in mammalogy as has already occurred in ornithology, where the concept of an order already has largely lost its significance; as a result the scientific aspect of systematics of vertebrates has suffered greatly.

In the classification of orders under consideration here, only one change has been made; i.e., pinnipeds have been treated as an independent order and not as a suborder of Carnivora. Based on the systematics of recent mammals, these two groups separate naturally—they are not less isolated than some other orders.

Based on already established views, Lagomorpha are treated here as an independent order (Weber considers them only a suborder of rodents). Hence, instead of the 18 orders of Simpson, we propose 19. Of these, 10 (52.6%) are represented in our fauna, one—the sea cow—is now extinct (Steller's sea cow).

The main subdivisions within the orders in most cases adhere to Simpson's scheme. By and large his classification is the most well

founded. Nevertheless, there are a series of deviations, some significant, mainly in interpretation of the content of the genus, which is understood more broadly than is generally the case. In our opinion this conforms better to the structure and principles of natural classification.

The systematic classification adopted is given in the chart below. Orders present in the USSR fauna are marked with an asterisk. (V.H.)

10

CLASS MAMMALIA

Subclass PROTOTHERIA

Order

MONOTREMATA

Subclass THERIA

Infraclass METATHERIA

Order MARSUPIALIA

Infraclass EUTHERIA

Cohort UNGUICULATA

* Order INSECTIVORA
 Order DERMOPTERA
 * Order CHIROPTERA
 Order PRIMATES
 Order EDENTATA
 Order PHOLIDOTA

Cohort GLIRES

* Order LAGOMORPHA
 * Order RODENTIA

Cohort MUTICA

* Order CETACEA

Cohort
FERUNGULATA

Superorder FERAEE

* Order CARNIVORA
 * Order PINNIPEDIA

Superorder
PROTUNGULATAOrder
TUBULIDENTATASuperorder
PAENUNGULATA

Order PROBOSCIDEA
 Order HYRACOIDEA
 * Order SIRENIA

Superorder
MESAXONIA

* Order
 PERISSODACTYLA

Superorder
PARAXONIA

* Order
 ARTIODACTYLA

Key for Identification of Orders

- 1 (2). Hind limbs absent; fishlike body with large bilobate caudal fins set horizontally CETACEA.
- 2 (1). Hind limbs present; body not fishlike and tail, if present, not in the form of a bilobate fin.
- 3 (4). Forelimbs in the form of leathery wings CHIROPTERA.
- 4 (3). Forelimbs of a different structure.
- 5 (6). Fore- and hind limbs very short and resemble paddles, i.e., all the digits entirely enclosed in a common integument PINNIPEDIA.
- 6 (5). Fore- and hind limbs of a different structure, not paddle-shaped.
- 7 (10). Feet possess hooves.
- 8 (9). Only one hoof on each limb. PERISSODACTYLA.
- 9 (8). On each limb, two large hooves and two small ones above them ARTIODACTYLA.¹
- 10 (7). Hooves absent (claws present).
- 11 (14). Between large chisel-shaped incisors and molars on jaws, a large toothless gap (diastema) occurs; its length not less than length of entire row of molars on corresponding jaw. Canines absent.
- 12 (13). Two incisors on upper jaw. RODENTIA.
- 13 (12). Four incisors on upper jaw; behind each large sharp incisor is located a minute blunt tooth. LAGOMORPHA.
- 14 (11). Diastema between incisors and molars absent or much smaller than length of molar row. Canines present.

¹ Limbs differ in structure in camels. The leg terminates in a broadened callused pad and true hooves are absent. There are two greatly broadened nails. Camels have not been included in this table as they are domesticated animals (wild camels are extinct).*

*It is now believed that wild populations of Bactrian camels still survive in China and Mongolia—Sci. Ed.

- 15 (16). Anterior portion of muzzle extended into well-developed small proboscis. Anteriormost tooth on each jaw, or only upper jaw, much larger than adjacent tooth.² INSECTIVORA.
- 16 (15). Anterior portion of muzzle does not form a proboscis. Anteriormost tooth on each jaw not larger than one next to it CARNIVORA.³

²If the structure of teeth is different, proboscis is always present and furthermore the front leg extremely short, feet very broad with huge claws, and set on edge with inner surface facing backward (moles).

³On the coast of the Commander Islands, skulls of the extinct Steller's cow—a member of the order of sea cows (Sirenia)—have been found. They are distinguished by upper and lower jaws measuring 60 cm in length, in which teeth or traces of them (alveoli) are absent (fig. 6).

ORDER OF SEA COWS,
OR SIRENIANS

Ordo Sirenia Illiger, 1811

*Superorder of Probosciforms**
Superordo PAENUNGULATA Simpson,
1945

Order of Sea Cows, or Sirenians

Ordo SIRENIA Illiger, 1811**

- 15 Mammals of large size, entirely monomorphic,*** highly specialized as typical aquatic animals. The species of this order represent one of the extreme degrees of specialization among mammals.

Body elongated, fusiform, and in general appearance, more similar to that of large dolphins, but as compared to the latter, and in relation to total animal size, the head is smaller and located on a short, movable neck not noticeable externally in all animals. In connection with the low mobility of the animal, the general body constitution is much heavier than that of dolphins and the body diameter in its thickest part is much larger. There are no external hind limbs. The hind part of the body is elongated and thins gradually, rather than abruptly, into a relatively thick tail region which turns into a wide, flattened horizontally oriented tail fluke, lacking internal skeleton (other than the vertebral column and the connective tissue). The posterior edge of the fluke forms a convex arch and the whole fluke is blade-like (Family Trichechidae—manatees), or else the posterior edge is deeply incised in the middle and the tail is bilobed (remaining families).

The anterior extremities are in the form of true flippers, without any [external] signs of differentiation into digits. Some species have nail rudiments on the II–V fingers (several manatees). The flippers are freely mobile in the shoulder joint and (in contrast to cetaceans) possess a considerable mobility in the elbow and hand articulations (see p. 30). The animal leans upon them, raises the anterior part of its body,

*In Russian original, *slonoobraznykh*; literally, “of elephant-like form”—Sci. Ed.

**Co-edited by Daryl Domning (D.D.), Howard University, Washington, D.C.

***Except *Dugong* — D.D.

moves, and performs other relatively complicated movements (arranging food in its mouth, etc.).

On the head, in connection with the peculiar structure of the skull (see below), the upper lip is extremely developed, forming with the nasal region a massive fleshy mass hanging down over the lower, normally developed lip, and represents a sort of wide, blunt and short proboscis. The mouth opening lies on the lower surface of the head. The shape of the "proboscis" varies in different forms (higher or wider), but in all forms it is highly movable, capable of changing its shape, and plays an important role in collecting food. In some animals (for example the manatees, *Trichechus*), the actively movable lateral parts
 16 can even mimic to a degree, a prehensile organ. It acts like the index finger and thumb of humans, and by bending it to the left and to the right the animal can grasp plants. The nostrils are located on the anterior upper part of the "proboscis"; they are crescent-shaped and closed (open only during inhalation and exhalation). The eyes are small and round; eyelids are devoid of eyelashes but richly supplied with special glands, secreting abundant viscous fluid that protects the eyes from the influence of water.¹ The Harderian gland is highly developed but, in contrast to cetaceans, the lachrymal glands are apparently absent. A sclera is not formed.* A well developed and highly movable nictitating membrane is present. The ears are located far behind the eyes and are represented by very small orifices; a pinna is completely absent.

The hair cover of the body is completely, or almost completely, absent and is represented by fine hairs scattered singly on the body, and having the structure and, apparently, function of sensory organs. This fulfills the need for high tactile sensibility of the skin, important for an animal living among aquatic vegetation in coastal zones. In the fetus, the number of these hairs is considerably greater. On the upper lip and partway around the mouth are found a large number of hairs; usually, however, they are short and do not form the "whiskers" characteristic of some pinnipeds. The majority of the hairs are elastic and bristle-like, but some are softer. Some hairs have a tactile function while others, especially the coarser ones, are considered a device for assisting the grasping of food with the upper lip.

¹In animals removed from the water, this fluid accumulates in the corner of the eye and then flows out. The legend of the "weeping sirens" has originated from this, and so does the name lamantin (from the French Lamentier; to weep). This oily liquid is, apparently, a product of Meibomian and Harderian glands.

*Meaning not clear—Sci. Ed.

In the majority of species, the skin has a very thick connective tissue layer (about 20–25 mm) and very thin epidermal layer (cuticle is about 0.1 of the total thickness of the skin). The skin [in manatees] is thicker on the sides than on the back as is characteristic of mammals in general; on the abdomen, it is approximately half as thin as that on the sides, but on the back, it is thicker than on the abdomen. Sometimes (Steller's sea cow, see below), the epidermal layer is especially developed and strong. In some species (Amazon manatee, *Trichechus inunguis*) the border of the caudal fin bears a hard cornification border (or is included in it) which may be detached and again re-formed.² The fatty layer is well developed.

The [skin] color is dark, more or less evenly brown, brownish or black in color; from below, it is lighter in some animals, and sometimes of a rare-meat color.

There are two mammary glands.

The female genital opening is slit-like, placed fairly far in front of the anal opening. The testicles lie in the abdominal cavity (far anterior, near the diaphragm); the male copulatory organ is long with highly developed corpora cavernosa, lies hidden under the skin, and contains no bony structures.

The skulls of all species of this order are completely monomorphic,* very peculiar and differ greatly in general structure from those of other mammals. They have some similarities with the skull of artiodactyls and perissodactyls, and particularly with those of elephants and hyraxes, but they sharply differ, in general and in details, from the skulls of cetaceans.

In its general features, the skull is characterized by the fact that the nasal openings are greatly shifted and directed upwards, and the premaxillae are large in size. In some animals they are very large and massive and are bent downwards in their anterior half (symphyseal part), taking on a beak-like form, and giving the skull a curved form 17 in side view (Hydrodamalidae, Steller's sea cow; and especially Dugongidae, dugong). In other forms, the premaxillae are less massive and extend forward, but are not, or are only slightly bent downwards (Trichechidae), and do not fuse together in a symphysis.** The nasal processes of the premaxillae extend far backwards, reaching the nasal bones. Together with the enlarged maxillary bones, they delimit the

²Judging by some figures of Steller's sea cow (see below), they apparently possessed such a structure on the posterior border of the fin.

*Except *Dugong*—D.D.

**Not true; symphysis is formed—D.D.

nasal cavity. The nasal bones are very small and shifted far posterior, forming [part of] the rear wall of the wide nasal opening, on the bottom of which the widely opened vomer is found. The nasal bones are sometimes absolutely rudimentary [or absent]. The maxillae are large, and the palate is long.

The supraoccipital is large, greatly extending forward, but not wedged between the parietals. The suture between the parietals disappears at an early stage and a single parietal is formed, constituting the cranial roof. The frontals are separated and with large supraorbital processes. The squamosal bone has a large zygomatic process, to which the jugal bone is connected. The space between the exoccipital and squamosal is only partially filled by the petrosal bone (petrosum); [the remaining space] consists of a large opening (filled with connective tissue in the living animal) leading to the cranial cavity. The tympanic bone (tympanicum) is quite closely connected [fused] to the petrosal bone, forming the petrotympanic bone (petrotympanicum). The tympanic bone is in the form of a fairly massive half-circle, but it does not form a bony auditory capsule (bulla). The petrotympanic bone is not fused with the skull but freely articulates and connects with the squamosal bone. The anterior and posterior lacerate foramina (for. lacera) are fused in a common large one. The lachrymal bone is small, not perforated, and in some animals it is connected with the surrounding bones. There is no lachrymal canal. The palate is long and the palatine bones, being small and shifted posterior, play a very insignificant role in its composition.

The mandibular bones are massive and heavy, connected in an elongate symphysial portion; they form a single bone. The anterior part of the lower jaw is recurved downwards, and the degree of its bending corresponds to the form and position of the premaxillae (most strongly in the dugong, and to a somewhat lesser degree in Steller's sea cow). The ascending ramus of the lower jaw has strong, well developed articular and coronoid processes, directed forward and of various relative size in various forms, and a massive broad angular process. There are no air cavities in the skull.

The dental system is highly peculiar and differs greatly from that of other mammals. The cheek teeth [in *Trichechus*]* are absolutely identical with a short crown carrying two transverse crests, each of which is formed from three tuberosities. During occlusional wear, the masticatory surface is flattened. The number of simultaneously functioning teeth in one jaw ramus of a mature animal is 3-4 or even 2

* D.D.

(*Dugong*) and from 5–6 to 8 (manatees, *Trichechus*). All the teeth are considered as true molars [some are deciduous premolars][†], and incisors, premolars and canines are absent. Only in male [and a few old female][†] dugong one permanent incisor erupts on each side of the upper jaw, converted into a peculiar small (up to 10 cm) “tusk”, directed downward.

With wear, the teeth [in *Trichechus*][†] are replaced by new ones, but not by the old tooth being pushed out by the new one growing under it. The newly formed teeth appear at the extreme rear of the tooththrows and at the same time the anterior ones (“old” teeth) fall out, the crowns having almost worn out and lost their roots, which are well developed in “younger” teeth. Accordingly, the tooththrow is continuously shifted forward. This

18 takes place because the posterior side of the bony septum between teeth (i.e. the septum between each two successive teeth) is resorbed, while on its anterior surface (i.e. adhering to the rear surface of the tooth in front) this bony septum grows forward. In manatees, replacement of teeth occurs throughout the whole life and the number of molars is, as a matter of fact, not limited. In manatees, for example, in every jaw quadrant (“half” jaw) not less than 30 teeth or possibly more³ are replaced throughout the animal’s life. If we take into consideration only the teeth functioning at a given moment, the dental formula for a fully

mature dugong (*Dugong*) is $I \frac{1}{0} C \frac{0}{0} P \frac{0}{0} M \frac{2}{2} = 10$, while in the case of

young animals of this species, it is $DI \frac{1}{0} I \frac{1}{0} C \frac{0}{0} DP \frac{3}{3} M \frac{3}{3} = 28^*$.

The biological significance of this unusual method of tooth replacement in manatees probably lies in the fact that in feeding on aquatic vegetation much sand** is obtained and the teeth are worn out relatively quickly.

[†] D.D.

³This manner of tooth replacement—from behind forwards occurs only in elephants.*** However, the number of teeth replaced in the course of life does not exceed 6 and only one tooth is functioning in each jaw ramus (in all 4 cheek teeth). Sirenians and elephants are also similar in that the tusks in both are formed by the incisors. The transverse orientation of the crests on the teeth in sirenians is similar to the corresponding structure in primitive Proboscidea.

*In Russian original, “ $I \frac{1}{1} C \frac{0}{0} P \frac{0}{0} M \frac{3}{3} = 26$ ” which is erroneous—D.D.

**Probably siliceous phytoliths in the vegetation—D.D.

***And some macropod marsupials—D.D.

Overall, a reduction in the dental system occurs in this order, and in one species (Steller's sea cow, *Hydrodamalis*) teeth are lost completely.

This reduction is connected with, and probably due to, the fact that in all species, in both the upper and lower jaws there are large elongated horny plates occluding with each other in front of the tooth rows. On the lower jaw, the plate is located on the symphyseal part which is bent downward, while on the upper jaw, the plate lies on the lower concave surface of its anterior part. Such a system is used for seizing and grinding food and has no analogue among other mammals. The small cornified part lying in the region of the anterior end of the premaxilla in even-toed ungulates has, however, some functional and morphological similarities to the upper plate in sirenians (see vol. I).

Owing to the great reduction of the skeleton of the posterior extremities, true sacral vertebrae are absent,* and not differentiated from the lumbar vertebrae; the caudal region is long. In the genus *Trichechus*, the number of cervical vertebrae is six.⁴ The number of trunk vertebrae in various species is 19–24; caudal—22–29, and 35 (*Hydrodamalis*, Steller's sea cow); ribs, 14–19 pairs.** Thoracic vertebrae are very

*True of manatees, but not dugongs — D.D.

⁴The number of the cervical vertebrae in other species cannot apparently be considered established. According to Weber (1928) there are 7, while Mohr (1957) stated that in the dugong and Steller's sea cow there are “?6 ?7”. Steller (1745–1753), who gave a detailed description of the Steller's sea cow anatomy, noted 6 cervical vertebrae.

The skeleton in the Zoological Museum of Moscow University has six vertebrae (V.G. Heptner), but it is possible that one is missing. In the skeleton found in the Zoological Museum of the Academy of Science (Leningrad) are seven cervical vertebrae (K.K. Chapskii), but it cannot be excluded that long ago in assembling the skeleton, some vertebrae might have been added to reach the number normal for mammals. A skeleton present in the Museum of Kiev University has seven vertebrae, but it is possibly more correct to consider them six; one thoracic vertebra may be placed with the cervical ones (A.P. Korneev). It is unlikely, however, that Steller could commit such a terrible mistake, and therefore it subsequently was agreed to consider the number of the cervical vertebrae in this animal as being six until further special investigation is carried out.

A solution of this problem based on museum skeletons is at the present time difficult, because all of them are actually composed of bones from different individuals. Only Evermann (1893) bought in 1891 an almost complete skeleton from the Commander [Islands] which was found “a short time” before that. The finder confirmed that the skeleton was found not far from the water's edge under a few inches of sand. The skeleton contained the complete set of cervical vertebrae which, after its study in the National Museum of Washington, was shown to be 7.

The deviation in the number of cervical vertebrae is a rare exception among mammals. Besides manatees, only the two-toed sloth, *Choloepus hoffmanni*, has 6 vertebrae, and the three-toed sloth, of the genus *Bradypus*, has 9 vertebrae.

**14–19 pairs among living species — D.D.

19 few and only 2–3 or 5 of the anterior ribs (Steller's sea cow) are connected to them, while the remaining ribs are free. Clavicles are absent.

The scapula is well developed and carries a normal spine. The articulation of humerus with scapula is quite free, the elbow joint is freely movable and the wrist joint has a considerable degree of mobility. Ulna and radius are separate and only in a few forms do they fuse distally in older animals.* In some young animals the whole set of carpal bones is present, but in mature ones, they fuse together into two or three large bones. The manus is pentadactyl and of normal construction; polydactyly is not found, and supernumerary phalanges do not normally occur in the species. Little is known, in contrast to cetaceans, of the structure of the forelimb skeleton in limiting their capability for different movements, such as acute bending of the hand in conveying food to the mouth, etc.

The skeleton of the hind limbs is utterly lost and only in a few species is there a totally insignificant rudiment of femur with an articulating head. The pelvis is represented by only the ischium and ilium, which are united together [in dugongids] into a rod-shaped bone in which its constituent elements are not well differentiated. There is no acetabulum.

The bones of the skeleton have no marrow cavities, and all of them, including those of the skull, are characterized by what is termed pachyosteosclerosis—Haversian canals are closed, all bone tissue is very compact resembling that of elephant bones, and shows conchoidal fracture. Moreover, the bones are relatively massive. All these features make the skeleton very heavy. Apparently, these features are of adaptive significance for animals living in coastal waters, bringing their specific gravity close to that of water, thus facilitating underwater submergence, etc.⁵

The kidneys are lobular as in true marine animals (whales, pinnipeds), the intestine is very long and exceeds the body length by 13–20 times, the large intestine is very long, only a bit shorter than the small intestine, and sometimes longer (Steller's sea cow). The caecum is well developed and in some species has accessory diverticula. The stomach is a complex organ, with a sharp constriction between the cardiac and pyloric parts, an additional blind sac or outgrowth in the cardiac region, and two blind sacs in the pyloric part.**

*Not true; in most they fuse both proximally and distally — D.D.

⁵Paleontological data show that pachyostosis appears in the evolutionary sequence during the transition to life in water.

**Actually part of duodenum — D.D.

The uterus is bicornuate and the placenta zonal.

With the exception of some differences in size and development of tusks in males [and females] of one species (*Dugong*), there is no sexual dimorphism.

The body length of smaller species reaches 200–300 and may reach 360 cm. Body diameter, in its thickest part, is about 150–155 cm (for a length of 203–247 cm) and the weight is up to 400–600 kg. In the largest species (Steller's sea cow), the body length reaches 800 cm, the diameter of the trunk about 620 cm and the weight up to 3200 (200 poods) and 4000 kg (morphological structure according to Weber, 1927, 1928; Mohr, 1957 and other references, and material in the ZMMU [Zoological Museum, Moscow University]).

They are specialized aquatic animals which do not come out on land,⁶ and are associated with shallows of coastal rivers, in particular with calm bays, lagoons, and river mouths, and with rivers rich in aquatic vegetation. They do not live far from shores, and particularly [do not inhabit] pelagic parts of the sea. Three species are purely marine, one marine and freshwater,* and one is strictly freshwater. Although most are inhabitants of tropical, warm water, one species inhabits the cold temperate zone. They are herbivorous forms, feeding
20 on submerged and floating aquatic plants ("grazing") along the shores. They are very sluggish, flaccid, and clumsy animals [on land] of quite low mental level. They are usually found in small groups. Young are usually single.

This order is widely distributed, the major part of its range being characteristic of littoral (coastal) marine animals and only in part characteristic of the ranges of animals associated mainly with the lower courses of larger rivers. Therefore, everywhere the range is typically linear (Heptner, 1936). The general range is divided into four isolated parts, differing greatly in their size—two lie in the Atlantic and two in Indian and Pacific oceans. These parts are not continuous, but divided into smaller and larger sections.

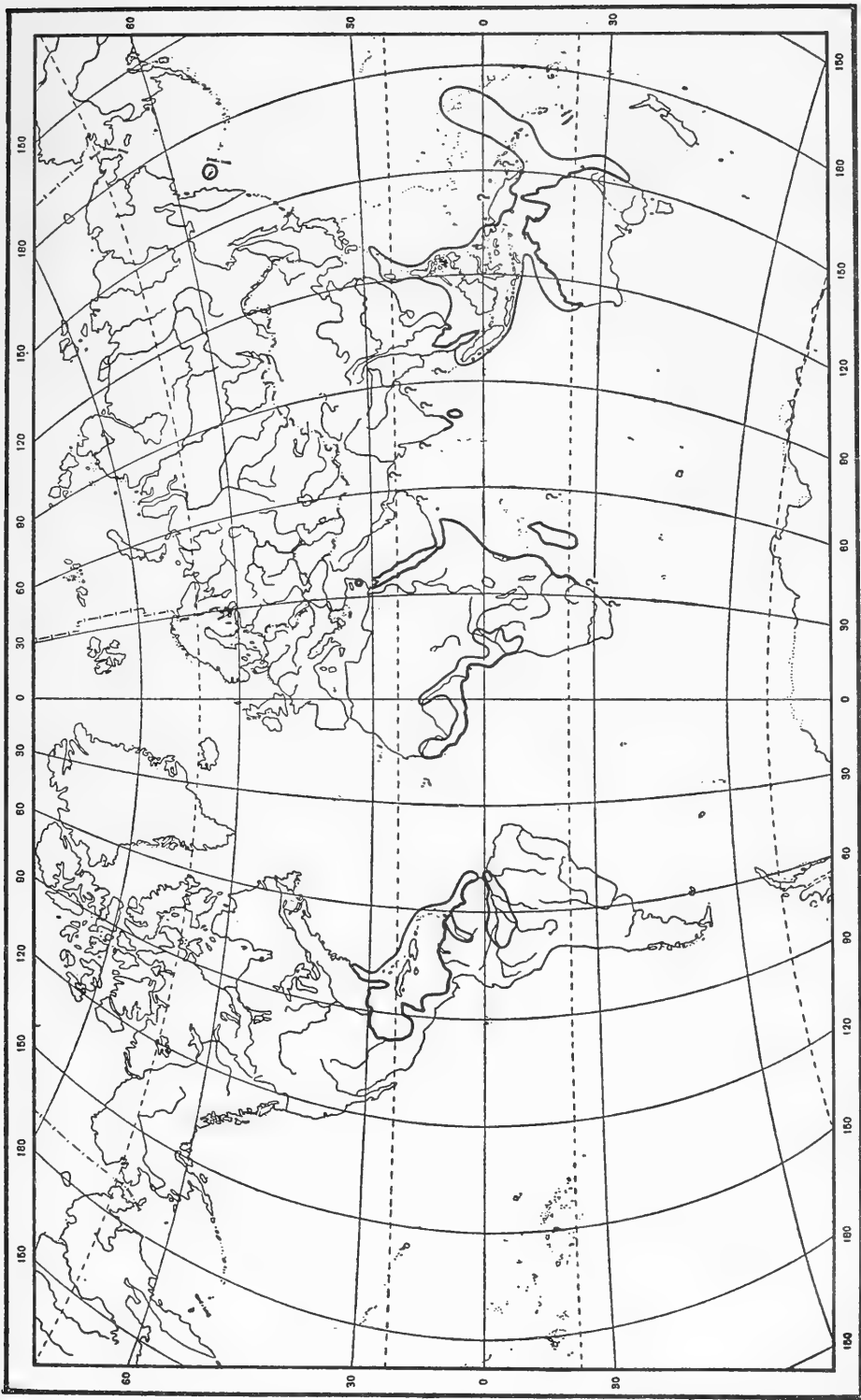
In America, the range (reconstructed, including transgressions in the north) extends to the southern coast of North Carolina (Wilmington)**

⁶If a sea cow is exposed on land or subjected to drying in some other way (for example, ebb-tide), it does not die of this, but as do whales, is "crushed" by its own weight and is overheated.*** However, these animals cannot move themselves on land.

*Two considered marine, and two both marine and freshwater—D.D.

**To New England—D.D.

***No evidence for this—D.D.



21 Fig. 1. Reconstructed range of the order of sea cows or sirenians, Sirenia. Question marks indicate the absence of information, but possible occurrence, at least previously, or doubtful data (South Africa, Mascarene Islands). The point in the eastern part of the Mediterranean Sea is an extralimital record of the dugong (*Dugong dugon* Müll.) on the coast of Palestine. V.G. Heptner.

and occupies the coasts of the Gulf of Mexico, islands of the West Indies, and Central America, as well as part of the northern and north-eastern coast of South America—the shores and river mouths in Colombia, Venezuela and Guiana to Cape Norte in the east (slightly southeast of Maracá Island, Brazil), lying somewhat north of the mouth of the Amazon. The range of this [partly] marine species of the West Indies (*Trichechus manatus*) does not, apparently, reach the mouth of this river.⁷ Moreover, the range in South America (of the freshwater species *T. inunguis*) covers the basin of Orinoco* and Amazon basin far to the west including, in any event, the region of a right-hand tributary of the Amazon, the Rio Madeira (according to the data of Hatt, 1934; G. Allen, 1942; Cabrera, 1960).⁸

At the present time the range is strongly modified and animals have been exterminated in most places, and north along the Atlantic coast, manatees are no longer found beyond the southern extremes of Florida,* and where they are protected.

In West Africa, the range occupies coastal lagoons and river mouths from the Senegal River on the north to the Cuanza River in northern Angola. The species inhabiting this region (*T. senegalensis*) lives in fresh [and salt] water and they penetrate upstream in the majority of West African rivers, especially the large ones. Thus, in the Niger, their range includes its left tributary, the Benue, but in the Niger itself, the range extends almost to Timbuktu. Manatees are widely distributed in the Congo basin.** Their upstream distribution along rivers is generally restricted by waterfalls and rapids. Reports and suggestions concerning the occurrence of manatees in Lake Chad and its basin are mistakes

⁷The range suggested by Cockrum (1962) is, apparently, not true even for the past. There are direct indications that owing to hydrological conditions (Murphy, 1936 and others), manatees did not occur to the east beyond the place mentioned, and were not found on the coast of northern Brazil east of the mouth of Amazon River. They did not reach Cape Sao Roque (the eastern point of the continent) and have not spread to the south, although, in the area southward from the Cape, along the eastern coast, the conditions for them were apparently favorable.*** Cockrum (1962) assumed that the area of distribution of these animals extended along the coast of South America to the mouth of the La Plata [River].

“Rio Madevia” and “Rio Madeva” given by Mohr (1957) are probably misprints instead of “Rio Madeira” (type locality for this species).

*Not true—D.D.

**No evidence for this statement—D.D.

***West Indian manatees occur in this region today—D.D.

lacking foundation,* as are data about the presence of manatees in the Great [Rift] Lakes of Africa.⁹

In the Indian and southwestern parts of the Pacific Ocean, the range of the dugong (*Dugong dugon*) occupies the greatly extended shoreline from East Africa and the Red Sea in the west to eastern Australia, the Solomon and Marshall islands, and the Ryukyu islands. The range in the above-mentioned areas was probably discontinuous from time immemorial, but because of inadequate information it is now impossible to reconstruct the true range. The range is divided at present into separate parts.¹⁰ Along the eastern African coast, the range extends in the south to Delagoa Bay at 26° S. Lat., a little south of Lourenço Marques, but in earlier times it may have been extended to the south (to the Cape of Good Hope?), and occupied the whole Red Sea along the southern coast of the Arabian peninsula, though not east of Aden. It occupies the coast of Madagascar, mainly the west and the small islands off the African coast (Mafia** and others).¹¹

Yet, the dugong is apparently absent and probably has not been present for a long time in the majority of places in the north of the Indian Ocean; i.e. the southern coast of the Arabian peninsula, in the Persian, Oman, and Bengal gulfs, and the shores of Indostan.*** The range here (the second part of the Indo-Pacific Ocean range) occupies only the most southerly part of the west coast of India, starting from Cananora (Canara [Cannanore], about 12° N. Lat.) southward and to the southernmost part of the eastern coast of the peninsula lying adjacent to Ceylon, which is included in the range.

The third part of the Indo-Pacific Ocean region occupied by sea cows is connected with extreme southeastern Asia, Australia and the islands lying between them. In the south, the range includes the western coast of Australia to the north of Shark Bay (about 25° S. Lat., a little

*There is now some evidence that manatees occur in the Lake Chad basin—D.D.

⁹Information concerning the occurrence of manatees in the past (about 1800) at Saint Helena Island in the Atlantic Ocean, which in its time provided material for zoogeographical speculation, is false and is probably based on the appearance of elephant seals (Hatt, 1934; Murphy, 1936).

¹⁰The range described here differs considerably from that presented by Cockrum (1962, map) which was incorrect at least in part. For example, the occurrence on the coast of Madagascar was not given although a series of reports were available.

**Off coast of Tanzania—Sci. Ed.

¹¹Concerning the Mascarene, Comoro and other islands of the Indian Ocean and the Mozambique Strait associated with Madagascar, there are no reports. Only Cockrum (1962) includes the Mascarene islands in the range.

***Archaic; Indian subcontinent—Sci. Ed.

south of Carnarvon), the northern coast, and the eastern coast south to Botany Bay (near Sydney). In the west, the range covers the Greater and Lesser Sunda islands. In the east, it covers the Solomon and Marshall islands (there are no definite records from other islands of Micronesia or Melanesia, in particular the Bismarck archipelago). In the north, the range includes Sumatra, the coasts of Malacca Strait (no definite records are known from the Nicobar and Andaman islands), the coast of the Gulf of Siam, the whole of the Philippine archipelago as far north as the Batan islands, Taiwan and the Ryukyu archipelago north to Amami-oshima (Amamioshima, 28° N. Lat.). Thus the range includes the southern coast and western extremes of New Guinea (concerning the northern coast, records are lacking), and the Molucca Island group. In this region, the range occupies the Coral, Arafura, Timor, Banda, Java, Flores, and Celebes seas, Macassar Strait, part of the South China Sea, i.e. all the internal seas lying between Asia and Australia, part of the East China Sea, the extreme eastern coast of the Indian Ocean, the extreme west part of the Pacific Ocean, and that part in the Micronesian region (Blanford, 1876; Allen, 1942; Carter, Hill, Tate,* 1946; Cockrum, 1962).

A distinct, very small part of the range lies separated from other parts in the Commander Islands [*Hydrodamalis* only].

A known event is the passage of a dugong through the Suez Canal to the Palestinian coast (Aharoni, 1930).

Remains of Tertiary sirenians (fam. Dugongidae) are known far from the present limits of the range—in Africa, Europe and even in Jamaica.

- 23 Sea cows, as was previously mentioned, are considered as a sharply characterized group, and thus, accepted by all modern investigators as an order. However, a short time ago, the sea cows were sometimes considered as a suborder (Sirenia) of the Order Subungulata, which, besides Sirenia, includes Hyracoidea, Proboscidea and the extinct Embrithopoda. Systematic and phylogenetic connections between all three contemporary groups is unquestioned—as was reflected in their combination in the Superorder Paenungulata (see p. xx). However, differences between them, even by evaluating all palaeontological data, are those normally recognized for ordinal rank. The differences between Sirenia and both Proboscidea and Hyracoidea are undoubtedly greater than those between Pinnipedia and Carnivora.

The systematic position of this order is, according to recent data, determined by their previously mentioned relation to Paenungulata. This

*Misspelled "Teg" in Russian original—Sci. Ed.

order has, apparently, more common features with the order of elephants and they can be considered as sister groups although the relation between them is quite distant. The nature of tooth replacement and some of its peculiarities, which is not elsewhere found among mammals, the transformation of incisors into tusks, some features of skull appearance and others, are among these common characters.* The similarity somewhat increases in the comparison of the more primitive ancient forms of both groups. Sea cows are sometimes considered closer to Hyracoidea. In any case, there is no doubt (and this is very obvious) that the sea cows have no relation either to pinnipeds or to whales. All the features common with whales are no more than convergences, and close study reveals deep principal differences between them. The greatest similarity with whales lies only in the general appearance, the absence of the rear extremities, and in some details characteristic of aquatic mammals in general.

In the eighteenth century, at the beginning of the last century and somewhat later, even competent authors (Pallas, for example) included the sea cows in the order Cetacea (whales) as a special group ("grass-eating whales"). However, even at that time, there were some indications not only of the independence of sea cows as an order, but also of their relatively closer relation to elephants. This point of view was, a long time ago, generally accepted, though it must be emphasized that the systematic isolation of this order is very sharp and that its relation to elephants is very distant. The same also applies to ungulates, though in the system of orders of the class, sea cows are always put between elephants (or hyraxes) and one of the orders of ungulates [see p. xx, this volume].

The order comprises two suborders: Trichechiformes, in which together with the extinct ones, all living forms are included, and Desmostyliiformes [now an order], including only extinct forms (one family with perhaps five genera). The systematic position of this group is, however, not completely clear, and some taxonomists consider it a separate order, Desmostylia, which is close to Sirenia.

The suborder Trichechiformes comprises five families, of which two (Prorastomidae — one genus, Protosirenidae — one genus) are extinct and three living: manatees, Trichechidae; dugongs, Dugongidae and kapustniks, or Steller's sea cows, Hydrodamalidae.** The family Trichechidae is,

*In part, no longer considered true — D.D.

**Now reduced to a subfamily of Dugongidae — D.D.

apparently, considered the least specialized among the existing ones. Species of this family have a relatively less developed, only slightly depressed anterior ("premaxilla") part of skull [rostrum], complete dental system, and 6 cervical vertebrae. The tail is blade-like and single-lobed. This group includes one genus, *Trichechus*. The family Dugongidae comprises four subfamilies: Halitheriinae (7 genera), Miosireninae (1 genus) and Rytiodontinae (one genus) are extinct, and the Recent Dugonginae with 1 genus *Dugong*. This last family is characterized by the considerable reduction of cheek teeth (to 2), the presence of tusks in the upper jaw of males, the extremely enlarged and sharply depressed upper jaw, and 7 cervical vertebrae. The tail is bilobed. The family Hydrodamalidae, kapustniks or Steller's sea cows, with 1 [recently extinct] genus, *Hydrodamalis*, is characterized by the complete loss of teeth, a fairly highly developed and depressed rostrum, and 6* cervical vertebrae. The tail is bilobed.¹²

Evidence on the origin of the group is given by representatives of the above-mentioned extinct families existing only in the Eocene, and the family Dugongidae which is represented by its extinct subfamilies in the Eocene—beginning especially from the Middle Eocene to Pliocene. The other existing families have no extinct representatives, or only their Pleistocene remains are known (manatees).

The oldest Middle Eocene forms, such as *Eotheroides*, though showing some essential differences from the existing ones (complete dental system, apparently, since they were characterized by the absence of horny plates, a fairly well developed pelvis, etc.), were true sea cows. They are well linked with the existing forms by means of a succession of forms. In the Middle and Upper Eocene, they were already very widely distributed and, therefore, the origin of this order must be related to the Paleocene. As was shown, the similarity in the structure of skull and teeth of the more ancient sea cows with primitive proboscideans and hyraxes is more evident than in the existing sea cows. The ancestors of

*Now known to be 7—D.D.

¹²The above-mentioned classification of the order differs from that adopted by Simpson (1945), mainly in the acceptance of Hydrodamalidae as a family (which he considers as only a subfamily of Dugongidae). This is partially determined by the fact that Steller's cows possess 6 cervical vertebrae and not 7.* Other authors consider this group also as a family (Weber, 1928; Mohr, 1957) even when there was the assumption of 7 vertebrae. The order of the families as regards increasing specialization is also changed. In sum of characters, the family Hydrodamalidae is closer to Dugongidae than to Trichechidae and is considered as a further development of this type. The difference in the number of cervical vertebrae sharply separates the families from one another.

A more thorough analysis of the extinct and existing forms and their relationship is given by Simpson (1932).

sea cows must, probably, be searched for among land forms, especially those which gave rise to the other Paenungulata, i.e. among the hyraxes (order Hyracoidea) and proboscideans (Proboscidea) as well as ungulates (Artiodactyla and Perissodactyla). However, direct "basal forms" of the order are not known.

The existing species in the order are 5. In the genus *Trichechus* L., 1758 (= *Manatus* Brünn.) there are 3 species: *T. manatus* L. (shores of the Americas—see above), *T. inunguis* Natt. (basins of Amazon and Orinoco*) and *T. senegalensis* Link (sea coasts and the lower reaches of the rivers of West Africa). In the genus *Dugong* Lac., 1799 (= *Halicore* Ill.) there is 1 species—*D. dugon* Erxl.** (the coastal region of the Indian Ocean and the adjacent southwestern Pacific). The kapustniks, or Steller's sea cows, *Hydrodamalis* Retzius, 1794—1 species—*H. gigas* Zimm. (coastal waters of the Commander Islands).

The greater number of species are endemic to the Atlantic Ocean, with two associated with its western coast and one with its eastern coast. One species is endemic to the Indian Ocean and small parts of the Pacific contiguous to it. The practical value of the group is insignificant. They are only hunted locally for their meat. In many places these animals have been extirpated and their number is limited almost everywhere. One species was completely exterminated (Steller's sea cow).

The USSR fauna comprises only 1 species, the kapustnik or Steller's sea cow, *Hydrodamalis gigas* Zimm., 1780—which constitutes 20% of the species of the order and about 0.3% of the number of species of our fauna (V.H.).

*Not found in Orinoco—D.D.

**Now attributed to Müller—D.D.

Suborder of True Sirenians

Subordo TRICHECHIFORMES Hay, 1923

Family of Kapustniks, or Steller's sea cow¹³

Familia HYDRODAMALIDAE Palmer, 1895

Genus of Kapustniks, or Steller's sea cow

Genus *Hydrodamalis* Retzius, 1794

- 25 1794. *Hydrodamalis*. Retzius. Kongl. Svenska Vet.-Acad. Nya Handl. Stockholm, 15, p. 292. *Hydrodamalis stelleri*.
1811. *Rytina*.¹⁴ Illiger. Abhandl. d. Berlin. Akad., 1811. p. 64. *Rytina borealis*.
1814. *Nepus*. Fischer. Zoognosia, 8, p. 640. *Nepus stelleri*.
1822. *Stellerus*. Desmarest. Mammalogie, pt. 2, p. 510. *Stellerus borealis*. (V.H.).

KAPUSTNIK, SEA COW, STELLER'S COW¹⁵

*Hydrodamalis** *gigas* Zimmermann, 1780

1780. *Manati gigas*. Zimmermann. Geograph. Gesch. d. Menschen und d. vierf. Thiere 2, p. 426.
1785. *Manati balaenurus*. Boddaert. Elenchus anim., p. 173.

¹³The characteristics of the family and genus are not given here, as they are clear from the characteristics of the order and the species description given below. Only the main generic synonyms are given.

¹⁴The first (and correct) spelling of the genus name. *Rhytina* is a later emendation.

¹⁵The name "kapustnik" [from cabbage] and "sea cow" are vernacular. The first originates from "sea cabbage"—a name which was and is still given to some seaweeds used as animal food.

"Steller's cow" is a literary name translated from a name of German origin.

*Misspelled *Hidrodamalis* in Russian original—Sci. Ed.

1788. *Trichechus manatus*, var. *β. borealis*. Gmelin, Syst. Nat., 1, p. 61.
1794. *Hydrodamalis stelleri*. Retzius, Kongl. Svenska. Vet.-Akad. Nya Handl. Stockholm, 15, p. 202.
1815. *Rytina cetacea* Illiger. Abhandl. d. Berlin. Akad., 1811, p. 70.¹⁶ (V.H.).

Description and Biology¹⁷

- 26 The body length of an adult animal exceeds 720 cm. The dimensions of the female killed on Bering Island on June 12, 1742 were as follows¹⁸:

“Body length from top of upper lip to end of right lobe of caudal fin	741.5 cm
Distance from top of upper lip to mouth angle	39.5 cm
Distance from top of upper lip to shoulder	132.5 cm
Distance from top of upper lip to genital opening	490.0 cm
Length of genital opening	26.0 cm
Tail length from constrictor muscle of anal opening to beginning of lobes of caudal fin	192.5 cm
Head circumference at level of nostrils	78.0 cm
Head circumference at level of eyes	122.0 cm
Neck circumference at occiput	204.0 cm

¹⁶The Commander [Bering] Island is the type locality of all of these names, based on the description of Steller.

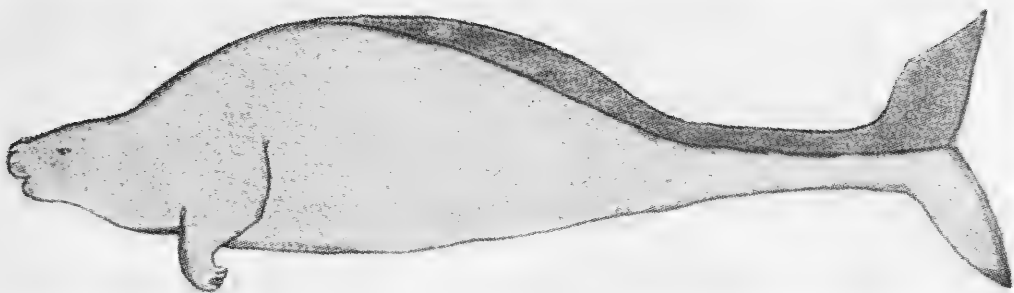
¹⁷The following description of the body structure and habits of the animal, written between quotation marks and without reference to author, is a translation from Steller (1751, 1753), done for this book.* This text is accurate and almost complete. Only a few parts, of interest only for Steller's contemporaries (concerning identity of his species to the American one, the possible movement of the animal on land, its use in medicine . . . etc.), the greater part of the anatomical section, some measurements (Steller gave 42) and other redundancies were left out. Data of other authors are given with reference to their sources.

The complete work of Steller, written in Latin and almost simultaneously published in German, has not yet appeared in Russian. Only small parts of it were recast or published in the form of free translations by S. Krashennnikov (1755) who had at his disposal Steller's manuscript. Steller's text was not always consistent. He wrote his famous work in Kamchatka or on the return journey to Petersburg. Steller died along the road through Siberia in Tyumen in 1746. It is possible, judging by the accuracy with which he kept his diary (1793), that at least part of the work was written on the island (V.H.).

¹⁸Translated from Paris feet (V.H.).

*But see also Jordan, D.S., 1899—D.D.

Height of anterior part (proboscis)	21.0 cm
Trunk circumference at shoulder	367.0 cm
Maximum trunk circumference halfway along posterior part of the abdomen	622.0 cm
Tail circumference at point of divergence of lobes of caudal fin	143.0 cm
Distance between ends of lobes or width of tail across lobes	199.0 cm
Height (thickness) of tail lobe	26.5 cm
Length of entire internal (upper) lip area which is covered by vibrissae or lip broom	13.2 cm
Its width [lip broom]	7.7 cm
Width of external upper lip in chin direction with its declined surface which is entirely covered with long white bristles	35.7 cm
Its height [external upper lip]	25.5 cm
Width of the lower lip, which is dark, without hairs or bristles, smooth, drooping on breast, heart-shaped	19.7 cm
Its height [lower lip]	17.3 cm
Distance from lower lip to chest	138.0 cm
Measurement or width of mouth from one end to other	52.0 cm
Width, or rather length, of stomach	112.0 cm
Length of intestine from mouth to anus	1521.0 cm
Accordingly it is 20.5 times longer than the animal itself (body length is more than twenty- four English feet as shown from the first measurement).	
Distance from genital opening to constrictor muscle of anal opening	20.4 cm
Diameter of trachea below larynx	10.7 cm
Length of heart	56.0 cm
Width of heart	64.0 cm
Length of kidney	80.0 cm
Width of kidney	45.6 cm
Length of tongue	30.6 cm
Width of tongue	9.0 cm
Length of teats	10.2 cm”



27 Fig. 2. Depiction of the kapustnik (Steller's sea cow) *Hydrodamalis gigas* Zimm., from the chart of the first officer of V. Bering's "Saint Peter", Lieutenant S. Waxell, in 1742. The drawing was probably made by G. Steller or is a copy of his drawing (from Pekarskii, 1869).*

27 According to Steller the number of vertebrae is 6 cervical, 19 thoracic, and 35 others. The skeleton present in the Zoological Museum of Moscow University has 6 cervical, 19 thoracic, and 32 lumbar, sacral and caudal vertebrae.

The skull dimensions of adult Steller's sea cows according to the material of the Zoological Institute of the Academy of Sciences and the Zoological Museum of Moscow University, are as follows: condylobasal length (12 specimens) 638-M 673–722 mm, zygomatic width (17 specimens including measurements of 8 specimens published by Stejneger, 1883–1884) 324-M 344–373 mm. The condylobasal length of the lower jaw (14 specimens) 432-M 465–491 mm.

Males were, apparently, somewhat larger than females and according to Stejneger (1883–1884) possessed somewhat wider zygomatic arches.** Thus his material (8 specimens) was divided into two groups: in one of them (probably males) the zygomatic width was larger than half the skull length from the upper end of the foramen magnum to the anterior point of the premaxillae, and in the second (females), these measurements are the same.

The length of the masticating plate (specimen in the Zoological Institute of the Academy of Sciences) is 182.4 mm, its width anteriorly is 80.5 mm, and posteriorly 81.5 mm. Its color is dirty, dark brown (in living animals the masticating plate was white in color—see below) (V.H.).

*Probably drawn by Plenisner; see Stejneger, 1936 — D.D.

**No specimens are of known sex — D.D.

“... The famous Clusius* considered this animal (Steller thought that he worked with the American “manati”, V.H.) clumsy and very ugly, because he saw only the hide stuffed with straw. The living animal was, actually, sufficiently distinctive. However, on account of its external appearance, and the style of movement, this animal is extremely striking. It has so thick a skin that it resembles the bark of an old oak tree rather than animal skin. The skin is black, rough and wrinkled as if covered with small pebbles, or resembles a shagreen, and is hard, elastic and devoid of hair; an axe or harpoon can hardly pass through it. Its thickness is about an inch (25.5 mm, V.H.) and, in transverse section and because of its color and smoothness, it greatly resembles ebony (black, V.H.) wood. This external cover is, however, not the true skin but rather its external layer (epidermis). On the spine the skin is smooth or bare. In contrast to this, it is covered, from the occiput to the tail lobes with annular wrinkles, making the skin somewhat uneven. The sides are very rough, as if covered with pebbles, carrying many convexities looking like sponges without peduncles (?). The skin looks disgusting, especially on the head. The described upper layer of the skin invests the whole body like a shell. Its thickness frequently reaches an inch and consists entirely of tubules, as in Spanish rattan or in Hindu and Chinese bamboo. These tubules adhere closely to each other as if united, and are so perpendicularly located that they can be separated along their whole length. Each fiber (“hair”, V.H.) lies and is fixed in the dermis at its lower end, is somewhat rounded, swollen and thickened, and has a tuberiform bulb, and therefore, the cut-off pieces of this upper skin have [when seen] from below many swellings like Spanish skin (Morocco ? V.H.). On the contrary, the upper surface of the dermis lying under it is, as in a thimble, entirely covered with small depressions in which the bulbs of the epidermis lie. Since these so-called tubules lie very close to each other, they are always wet and swollen, but if this upper layer of the skin is horizontally cut off, nothing is excreted from the tubules and the cut-off surface is entirely smooth, similar to a cut piece of claw. However, when these pieces are dried in the sun, cracks are formed and the whole piece may be broken like a piece of bark and the whole structure of the skin, in the form of distinctive tubules, is quite obvious. Through these tubules, a liquid or watery mucus is excreted, which is more on the head and side and less on the back. If the animal lies for some hours on the dry shore the back becomes completely dry,

*C. Clusius, 1605, *Exoticorum libri decem*, Leiden — D.D.

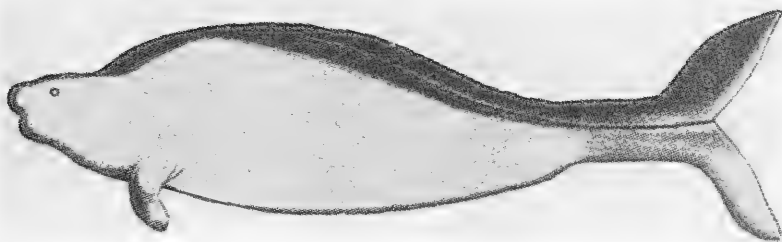


Fig. 3. Depiction of Steller's sea cow from "Zoographia", P.C. Pallas (1811). The drawing is, probably, a copy from the figure of S. Waxell (see Fig. 2) and described by Pallas as a "draft".

while the head and side remain wet or moistened. Thus, the thick upper layer of the skin on the animal performs two functions: when the animal occupies places with sharp stones, or when in winter it is always found in the midst of the ice, it does not strip off its dermis during feeding, or when strong waves strike the animal against rocks and submerged stones, which I myself often saw, it does not die, but on the contrary, is protected as with armor. On the other hand, in summer and as a consequence of the very high evaporation, the animal does not lose its heat and in winter, with extreme cold, it can survive. This occurs because the animal cannot stay under water for a long time, like other water animals and fishes, but during its feeding, half its body must be above water, and subjected to the effect of cold.

According to my observation of many dead animals that were cast up by the sea, these animals died because their external skin layer was damaged by rocks; this occurs mainly due to the ice in winter.

In addition to this, I have frequently noticed that when the wounded animals were pulled by harpoons to the bank, they struggled very furiously by their abdomen and tail while being supported by their forelimbs, and thus large pieces of the external skin layer were detached. I also noticed the detachment of these layers from the forelimbs or hands and from the so-called hoof (hand, V.H.) as well as from the lobes of the tail, and this confirmed my opinion . . ."

"... some sea cows had on this upper skin layer fairly large white spots and stripes and therefore the skin appeared speckled and this color penetrated through to the true skin [dermis].

29 The upper skin layer on the head, around the eyes and ears, on the mammary glands and arm-pits, possessed a tuberculous (stony) form or the form of shagreen, and was thoroughly filled with harmful insects

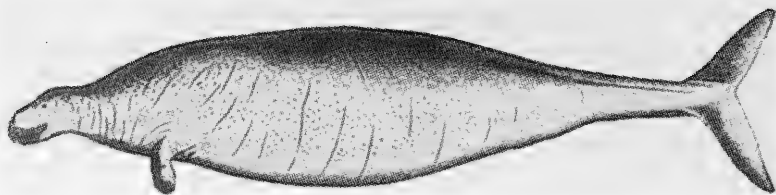


Fig. 4. Depiction of Steller's sea cow assembled by J.F. Brandt (1846) and identified by him as an "imagined picture" ("Icon idealis"). The skeleton of the animal was not known at that time and Brandt had at his disposal only fragments of the skull and masticating plates.

which grow round the skin.¹⁹ Very frequently, the latter appeared to be perforated by these insects, and even the true skin [dermis] was injured. If this occurs, the oozing lymph of the penetrated glands, in which there are usually vesicles containing fat, forms large, thick protuberances similar to those on whales, and such patches make the body ugly.

Under this previously described upper layer of skin there lies around the whole body the true (actual) skin [dermis]. Its thickness is two lines (about 5 mm), soft, of white color, very compact and firm, resembling that of a whale in respect to its structure and thickness, and perhaps required for the same purposes.

The head, as compared to the huge body, is small, short and where it ends is not evident; it is long and almost quadrangular in form; however from the crown to the lower jaw, it broadens. The crown itself is flattened, and its black superficial skin has bumps (stony, V.H.), or looks like shagreen and appears almost broken; it is thinner (by 1/3) than in other places, and is easily separated. From the occiput to the nostril, the surface is bent and again bent from the nose towards the nostril as far as the lips. The anterior proboscis (the protruding part of the upper lip, V.H.) has a length of 8 inches (20.5 cm) and, from the nose to the occiput, it is strongly thickened.

The shape of the mouth (opened mouth) does not pass backwards, but is located along the sides. The external lip is so large, and declines to the angles of the face and extends far above the lower jaw, that if one examines only the head, he thinks that the shape of the mouth opening extends backwards, but at a very low level.

¹⁹An amphipod crustacean — *Cyamus rhytinae* Brandt. (V.H.).

The opened mouth is small in relation to the animal's size; however, it need not be large because the animal feeds only on seaweeds and lives on them.

Both upper and lower lips are paired, and divided into external and internal regions.

The external upper lip protrudes obliquely forward as the most anterior part of the proboscis and has a semicircular form. It is flattened, swollen, thick, 14 inches (36 cm) wide and 10 inches (25.5 cm) high, white in color, smooth and covered with a large number of tubercles or cones. From the middle of each tubercle grow white transparent bristles, 4–5 inches (10–12.5 cm) long.

The internal lip is 5 inches (14 cm) long, $\frac{1}{3}$ inch (8 mm) thick,* completely separated from the external one and united with the external lip by its base only; it hangs over the palate like a calf's tongue (!), is all tattered and is hard, like dry twigs of a broom. The above-described upper lip tightly closes the mouth from above, is mobile, and
30 is used to browse on seaweeds in much the same way as horses and bulls collect their food by sliding the lips apart and extending them forward.

The lower lip is also paired. Externally it is black, smooth, without bristles, of irregular heart-shaped form, and sometimes looks like a chin, seven inches (18 cm) wide and six and eight-tenths inches (17.5 cm) in height. Internally, the lower lip is only slightly separated from the external one, is rough and when the mouth is closed, it is not seen at all because the arch-shaped external lip lies under it; however, the internal lower lip adheres to the internal upper one and tightly closes the mouth.

Where the lower jaw adjoins the upper one, the space remaining between them is occupied by numerous dense and thick white bristles one and one-half inches (38 mm) long. This prevents anything from being dropped from the mouth during mastication, or washed off by sea water: the water, which together with food is always taken into the animal's mouth, is drained outside when the mouth is closed.

The above-described bristles have the thickness of a goose feather quill, white, hollow, and with follicular swellings from below. By them, it is clear to see without a magnifying glass how nature forms our hairs.

When the animal lies directly on its abdomen, the height of the anterior part of the proboscis or muzzle, measured perpendicularly

*From Steller (1753)? Steller (1751) reads " $2\frac{1}{2}$ inches wide"—D.D.

from the nostrils to the lips, is equal to eight inches (20 cm); it extends from the nose to both the anterior-most part of the lips, and to the lateral side of the upper jaw, like mesenteries (in folds), anteriorly rounded, then thickens and its size greatly increases. The external lips are very greatly enlarged, thick, as if swollen and, as in cats, carry many white pores (!) or orifices. From each, thick white bristles protrude which become thicker as they gradually approach the mouth opening.

The thickest bristles are those growing between the lips of both jaws. They use these bristles in browsing seaweeds, and they prevent anything from falling from the mouth. The lower jaw is shorter than the upper one and is movable. The lips of both upper and lower jaws are mobile and function as in our draft animal [horse]. When the animal picks vegetation with its hands or forefeet from the plants growing underwater on the stony bottom, it cleans the fronds from the hard stems and roots (which are not utilized as food) with the above-described bristles as if cut off with a blunt knife. These stems and roots are thrown up by the waves during [high] tide and heaped on the shore in very large piles, indicating that an animal is present. Since the stems of aquatic plants are much harder and thicker than those of terrestrial plants, these beasts must have harder, more compact lips than any terrestrial animal. Therefore, such lips are not utilized by man as food and they are not softened by boiling or any other means. The inner lips are so constructed that, if they are cut open, separate small areas are seen on them similar to those on a checkers or chess board. These are innumerable, very small and thick red muscles of rhomboidal or trapezoidal shape. Between these muscles numerous areas resembling tendons are located, and form a net or tissue of vesicles filled with liquid fat. These lips easily release all their fat when cooked in boiling water and when they are defatted, all the white areas look like the numerous tendons of a net. This natural structure, it seems to me, has three purposes, namely:

- 1) in order to make the lips stronger and more compact and protect them from external injury;
- 31 2) in these muscles the heads and tails, i.e. their beginnings and ends [origin and insertion] are so located that their heads are slopingly directed toward the mouth opening while their tails, or ends, are located obliquely in relation to the parietal, in such a way that their beginnings and ends form a sort of garland and this helps raising and moving the heavy lips;
- 3) with the assistance of this structure, the lips can be, to a certain degree, bent in a helix or spiral and since the whole head is covered by

a thick cortex it bends with difficulty and thus, when the animal wishes to browse on elastic seaweed, it is not necessary to move the whole body.

Mastication in these animals occurs in a manner different from other animals. It is achieved not by teeth, because they possess no teeth, but with the assistance of 2 long bones found in their place. These bones [masticating plates] are large, of white color and are considered as whole rows of teeth or as one tooth mass. One of these bones is fixed to the palate, and the other to the lower jaw.

These bones are, however, attached in an entirely unusual manner and the method of their attachment cannot be attributed to any of the known ones. They cannot be described as fixed because they do not insert in the jaw as do teeth, but their protuberances and pits lie in corresponding protuberances and pits in the palate and lower jaw.

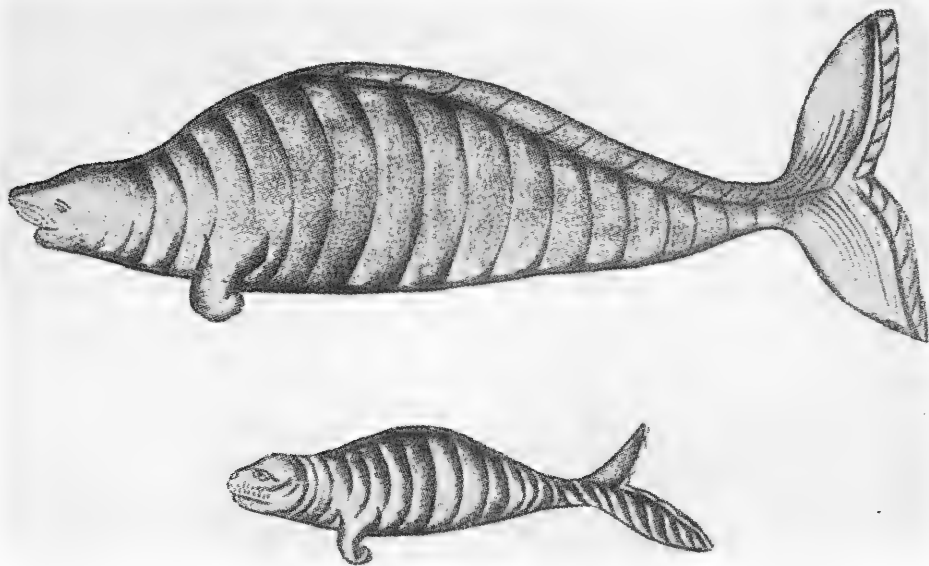


Fig. 5. Depiction of Steller's sea cow made from the so-called "Royal Agriculture Manuscript" of S. Waxell and his later (compared to that described by Pekarskii, 1869—see Fig. 2) chart (Bikhner [Büchner], 1891). In the original, the upper drawing has a length of 26.5 cm (in that of Bikhner, 1891—from the nose to the engraved tail 20 cm), and two times more than the lower drawing. The upper drawing ("Royal Agriculture Manuscript No. 2") is, apparently, a more detailed drawing of the same animal in Fig. 2. The lower drawing ("Royal Agriculture Manuscript No. 1") was greatly changed during re-drawing, probably by the same source (according to Bikhner, 1891—this is a depiction of another animal).

Moreover, the dental bones are fixed in the anterior part of the hard skin of the inner upper lip, along the sides of the mouth in the edge of the bones, and are finally inserted into the palate and lower jaw in the posterior part by means of a double outgrowth, and that is how they are attached.

32 These grinding bones occupy the place of all molar teeth and, like a thimble or sponge, have many small holes on the lower surface through which, as in the teeth of [other] animals, the arteries and small nerves pass dorsally; these dental bones are far from smooth and covered with numerous bent wavy grooves; between them prominences are raised which, in their turn, occlude during mastication, into the grooves of the opposite dental bone and between them, and the marine plants are ground as in a hand or fulling mill.

The nose lies on the uppermost part of the head and to the sides as in a horse; the two nostrils are separated by the nasal septum of one and one-half inches (38 mm) in width. The nostrils themselves are 2 inches (51 mm) long and the same in diameter; they are open, but inside, there are many flexures or blind pockets. The inner walls of the nasal openings are extraordinarily thick, wrinkled and covered with compact skin with many black pores which have bristles protruding from each of them. These bristles have the thickness of sewing thread and are one-half inch (13 mm) long and are easily detached; they perform the function of those in other animals.

The eyes lie exactly mid-way between the end of the muzzle and the ears, at the same height as the upper part of the nose or slightly higher. They are relatively small in comparison to the large body of the animal, and are not larger than those of sheep. Externally, they have no eye-lashes or any similar structure surrounding the eyes, and they protrude from the skin through a rounded hole, which according to my measurements, has a diameter of scarcely one-half inch (13 mm). The iris is black in color and the eyeball is yellow blue. The corners of the eyes are not noticeable; moreover, when the skin around the eyes is cut off, a cartilaginous body like a cock's comb protrudes at the large (anterior) corner, as in the case of the sea otter. When needed, this body closes the eye, nearly in the same way as in animals which are grazing, i.e. searching in dusty and dirty soil, and has such a membrane (third eyelid, V.H.), which can be stretched by the animal on the eyes to prevent the entrance of any harmful objects. This cartilaginous body forms, with its other side, the wall of the lachrimal sac and is connected with it by a common compact skin. On cutting into the lachrimal sac,



Plate 1. Steller's sea cow, *Hydrodamalis gigas* Zimm. Painting by N.N. Kondakov.

dense mucus is found inside; the lachrimal sac is large enough to allow the entrance of a chestnut, and it is lined by glandular skin.

Externally, the ears are represented by a small, open orifice but there are no traces of external ears. The ears themselves are unnoticeable, unless a person searches carefully for them. They cannot be differentiated from the surrounding skin which resembles shagreen. The shaft of a feather can hardly pass into the ear.

The internal ear canal is smooth and coated with an extraordinarily smooth (polished) black skin, and therefore it can be easily detected, when the muscles of the posterior part of the head are separated, by its color.

The tongue is 12 inches in length (30.5 cm), its width three and a half inches (9 cm), and as in cows, it is pointed at its end; its surface is rough as a file and covered with low warts. The tongue is so deeply placed in the mouth that one may doubt its presence. If it is pulled by hand from the mouth, its anterior part fails to reach the grinding plate of the mouth by one and one-half inch (38 mm). However, if the tongue were as long as in other animals, it would interfere with the above-mentioned wide bones during mastication.

The head is not visibly demarcated from the neck, and these are similarly connected to the trunk without any demarcation in any place, and thus the body is constructed as in a fish. The neck is not clearly demarcated, except that it is half the length of the head, elongated, round, and somewhat more slender than the posterior part of the head. In spite of that, the neck is movable due to the presence of movable vertebrae. However, these movements are only observed during feeding in living animals. During this, the animal lowers its head as does an ox, grazing in a dry pasture. However, if the animal lies resting or after being killed, the animal seems to have an immovable neck owing to its
33 thick clumsy outer skin and especially due to the absence of any external trace of the cervical vertebrae.

From the scapula to the umbilicus, the trunk is again strongly thickened; and from the latter to the anus, the trunk size decreases and it again becomes slender. The flanks are as bulging as the belly itself, and the latter, due to the great weight of the intestine included in it, is very swollen, stretched and distended by the intestine. From the umbilicus to the anus, the trunk is thinned to the same degree as from the chest (mammary glands) to the neck.

In spring and autumn, when the sea cow is in fat condition, the back is somewhat convex, and in winter when they are emaciated, the back

appears flat, and on both sides of the vertebral column there appear deep hollows; and thus the vertebral column and vertebrae are clearly seen.

The ribs are curved up on both sides of the spine as a convex arch and in those places where they articulate with the vertebrae, as in the case of human beings, they again bend down forming an arch, where on both sides of the vertebral column they form a double groove along the whole length of the back.

The tail starts at the 26th vertebra; the caudal vertebrae are 35. Posteriorly from the anus and in the direction of the tail fins the tail becomes thinner and not completely flat, but rather somewhat quadrangular . . . the tail muscles fill the empty places in the vertebrae and the angles between their processes by 4 plates and therefore, the tail looks like a long quadrangle with blunt angles.

The tail is generally thick, extremely strong, very hard, stiff (slightly movable) and ends in a black fluke. The latter is not divided into rays but forms a single unit. Its material is similar to the whalebone (baleen) which is used by the dressmakers, and, similarly, is composed of leaves lying one above the other as rings of a tree or the grain of a piece of wood. At a distance of one-quarter from the end, it appears wider and somewhat resembles a coarse spindle*. . . . The fluke itself, forming the tail end, has a width or length of 78 inches (199 cm), a height of $7 \frac{3}{10}$ inches (18.5 cm), and a thickness of 1.5 inches (38 mm). . . .

The caudal fluke somewhat resembles pincers (?), with horns or hands of equal size. . . . The tail blades are located, as in whales and dolphins, to the sides, and are not, as in the majority of fishes, in a line with the spine. If the sea cow slowly moves its tail to one side, it slowly swims forward, but if it strongly moves the tail upward and downward, it rapidly swims forward and tries in this way to move away from harmful hands wanting to pull it on to the shore.

The most remarkable thing in which this animal differs from all terrestrial animals which live in water and from aquatic animals which spend some time on land, and from all animals in general, is its entirely unique hand or fore limb, if it can be so called. At the neck, two limbs originate straight from the shoulder bones, 26 inches (68 cm) in length and consisting of two parts. The uppermost bone [humerus] is connected to the scapula by a flat articulation.

Here, as in the case of humans, there are radius and ulna, both of which border on the carpal bones with the metacarpal bones (called

*In Russian original, "osti kolosa"; literally, grass awn—Sci. Ed.

metatarsals and premetatarsals, V.H.), but neither fingers, nails nor claws can be detected. The above-mentioned anterior and middle (metatarsal and premetatarsal) parts of the limb are covered with dense fat and coated with many ligaments and superficial skin, and have the form of the newly overgrowing skin on a wound on the human extremity. However, the skin and especially its superficial layer is thicker on that part and also harder and drier, so that the ends of the hands roughly resemble a kind of crustacean claw [nail] or horse-hoof, even though the horse-hoof is sharper and narrower and therefore more adapted to
 34 digging, or scraping. At the posterior border, these limb ends are smooth and curved; from below, they are, to a certain degree, concave (empty) and covered with numerous dense bristles about one-half inch (12–13 mm) in length and, when scratching, are as sharp as the twigs of a broom. In one of these animals I noticed nipper-like limbs, divided into two parts, similar to the cow hoof. However, such division was not an actual one and was restricted to the superficial skin layer, and was probably accidentally brought about and not naturally created in this form. This is still more possible, as the superficial skin layer lying on the so-called claw handle is very dry and may be easily cracked.

This Platonic man, as the famous Raiyus (Ray, V.H.)* said in jest, used its hands in different manners. It can use them as fins in swimming. It walks on them in shallow waters as on legs; it holds itself upon them, resting among the slippery submerged stones and rocks, and scrapes and tears off the sea plants and seaweeds from the rocky bottom as do horses with their forelimbs. It can lean upon them and thus make great resistance when wounded by a harpoon and dragged from water to the shore. In such conditions, it holds so strongly that the upper layer of skin on the hand is split and torn off in pieces. During sexual intercourse, the female lies on her back and swims in this position. The male lies upon her; she holds the male strongly and he, in his turn, embraces her.

On the anterior part of the breast, two teats are found, located in a manner different from that in other animals. Each one lies under the corresponding arm as in the case of humans and has a similar appearance. Each breast has a length of 1 1/2 feet (45 cm), is convex, and bears many folds or spiral flexures directed inwards. The breast is glandular, extremely hard, harder than the cow udder and without fat deposits. The fat layer covering the whole body is found also on the

*John Ray—D.D.

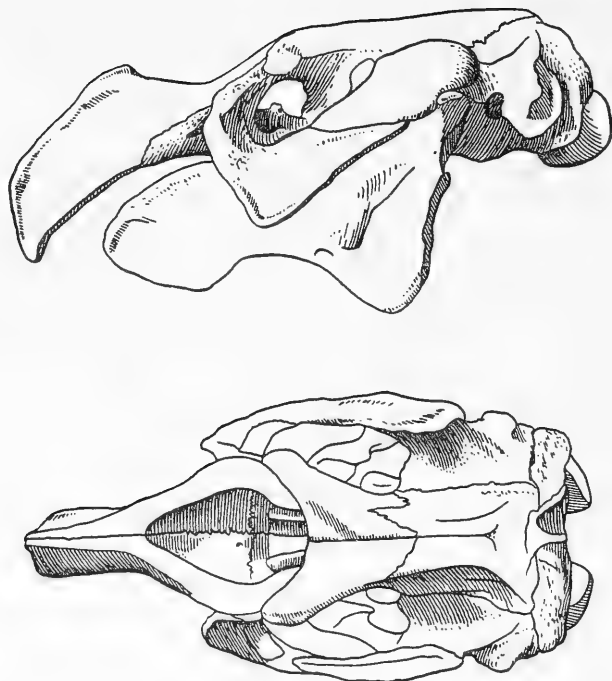


Fig. 6. Skull of Steller's sea cow. Upper figure, side view of skull; lower, dorsal view (from Stejneger, 1884).*

breast and is as thick there as on other parts. However, the upper layer of skin is thinner, softer and more wrinkled. The nipple also is of dark outer skin, with circular wrinkles. However, this superficial skin layer is soft; the nipple hangs under each hand or shoulder; in lactating animals, it has a length of 4 inches (10 cm) and a thickness of 1.5 inches (38 mm). If the lactation period is over or if the animal has not yet given birth, the nipples do not protrude and are so short that they can be considered as accidentally occurring warts. At that time, the breast also is not very swollen. The milk of these sea cows is as sweet
 35 and fatty as regards its taste and density, as that of sheep. Frequently, I drew milk from nipples after the death of the animals, as from cows. The area around the nipple is very wrinkled and a little raised above the surface of the breast. In each nipple there are from 10 to 12 milk ducts which open into the teat. The boiled mammary glands were somewhat harder than a cow's udder and they had a weak gamy taste.

*Actually from Simpson (1932) — D.D.

These animals mate in the same way as human beings. The male lies above and the female lies below. The penis is 32 inches (81.5 cm) in length; it is tightly fixed to the belly wall by its sheath, reaching the umbilicus; it is thick and ugly in its external appearance. It is similar to that of the horse and has the same head, but is somewhat larger.

The female genital opening is located eight inches (20 cm) in front of the anus. Anteriorly, the opening is nearly triangular . . . to the rear it narrows. . . . The anus . . . is closed by a constrictor muscle, not very tightly. Its width is four inches (10 cm); the sphincter is white. . . .”

From the biological observations of Steller given in the part of his work entitled “Description of behavior and nature of this animal”, the following lines deserve particular attention (many interesting observations are not directly related to the biology of this beast). “. . . I was lucky enough, or rather unfortunate, to be obliged to observe the behavior and customs of this animal in front of my door for ten months²⁰ and thus I wish briefly to state that I can explain [their behavior] with trustworthiness.

These animals like shallow and sandy places on the shore. However, they very willingly stay where rivers and creeks pour into the sea, and on their banks, as they are attracted to the fresh water coming to the sea; therefore, they stay there in groups. When they feed, they lead their young or the newly born ones in front of them, following them from behind and on the sides, and very carefully surround them, keeping them in the center of the herd. When the tide rises, they come very near to shore, so that I could not only beat and prick them, but sometimes even stroke them with my hand on their back. If they suffer from
36 a severe pain, they only moved away further from the coast than usual, but they soon forget that and come near again.²¹

37 Usually, their whole families are found close to each other; the male with the female (“with his wife”), with one adult [offspring?] and also some other young. Each husband, apparently, does not have more
38 than one wife; they give birth to young at any time of the year, but most often, judging by the newly born young, in autumn. Proceeding from

²⁰Bering’s ship “Saint Peter” escaped a rock and was very lucky to be thrown on the flat shore of a broad bay, where the crew spent the winter in mud huts and where Bering himself died. This place was very favorable habitat for sea cows (V.H.).

²¹Steller writes elsewhere “. . . it is rather possible to believe that it is possible to make this animal tame, rather than this strange cunning which is attributed to it in stories (spoken about the American species, which Steller considered the kapustnik, V.H.). Due to its extraordinary stupidity and greediness for food, this animal is tame by nature, and there is no necessity to domesticate it . . .”.



35 Fig. 7. Bering Island, shore near Cape Manati. Former habitat of Steller's sea cow.
Photograph by S.V. Marakov.

the fact that I observed their mating early in spring, I think that pregnancy lasts more than one year, and that they give birth to no more than one young, which can be deduced from the short uterus and the fact that the adult female has only one pair of nipples. Moreover, I have never observed more than one calf beside its mother.

These insatiable animals eat continuously. They are extremely greedy for food, so they hold their heads all the time under water; accordingly, they very rarely worry about their life and safety, and it is easy in a boat or even swimming naked among them to choose which one is needed to remove from the sea. During feeding they do nothing but thrust their nose out from water every four or five minutes, and, making a noise similar to the neighing, sniffing, and snorting of horses, they breathe out air with a small amount of water. During feeding, they put one leg after other and in this way they swim slowly, or walk like oxen or sheep. Half of the trunk, mainly the back and flanks, are always protruding from the water. During feeding, sea-gulls sit on their backs and pick the lice (crustaceans, V.H.) found on the upper layer of the skin and in this way they are useful to them, in the same way as crows do on swine and sheep. The sea cows do not eat all the types of sea weeds without selection, but they mainly eat: 1) wrinkled cabbage, like Savoy cabbage with latticed leaves; 2) water plants with upper parts similar to a cudgel; 3) plants which look like the whips of ancient

Romans; 4) very long sea weeds with a wavy vein edge.²² In places where these animals were feeding, even for one day, the roots and stems thrown out by the sea lie on the shore in large heaps. After they feed to satiety²³ some of them lie on their back. To avoid being on dry land during ebb-tide, they swim away from shore farther into the sea.²⁴ In winter, these animals frequently die under the ice which floats along the coast, and dead animals are cast up onto the shore by the sea. The same also happens when the waves strongly strike the rocks, taking these animals with them. In winter the animals are so emaciated that all their ribs can be counted along the vertebrae.

In spring, they come together as do human beings, mainly in the evening when the sea is calm. However, before copulation they show many amatory signs in their relation to one another. The female slowly swims in the sea here and there, and the male follows her all the time; the female moves around for a long time near the male until she reaches extreme sexual desire. She then lies on her back as if she is tired and does that seemingly unwillingly. When this occurs, the male almost in a frenzy rushes on her, and they copulate with each of them embracing the other.

Capture is carried out with the help of a large iron hook, one end of which looks like a ship's anchor (having a hook directed back-
 39 wards); while the other end has an iron ring to which a very long and strong rope is connected. A very strong man held this hook (harpoon V.H.) and sat with four-five persons aboard a boat. One of them handled the tiller while the other three or four rowed; and with them he carefully approached a whole herd of these animals. The hunter

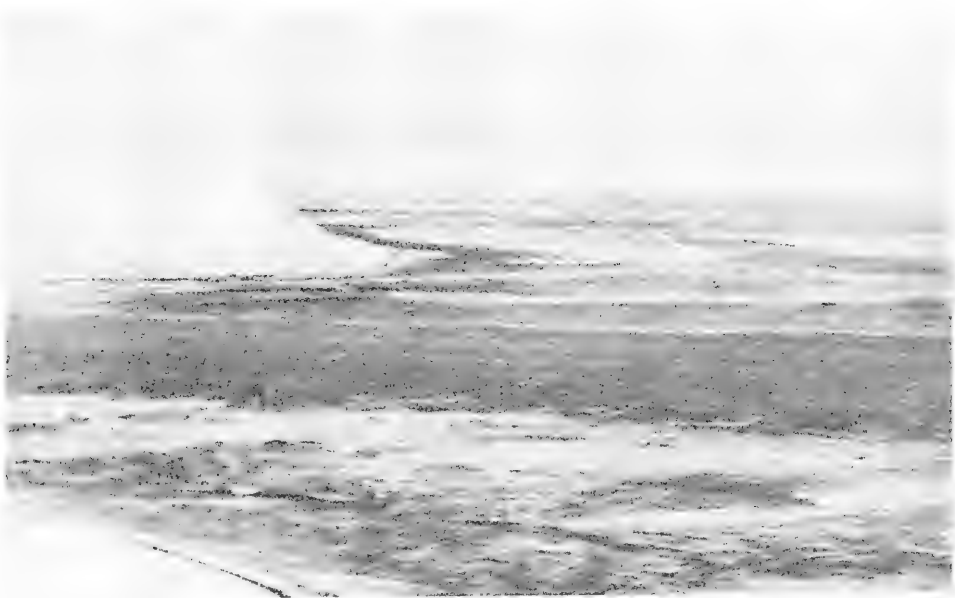
²²According to the opinion of A.V. Vozzhinskaya (Institute of Oceanology of the Academy of Sciences), Steller wrote about the following species in order: *Agarum* sp.; *Nereocystis* sp.; *Alaria* (*fistulosa*); *Zostera*, or *Laminaria longipes*.

²³Steller writes elsewhere that the intestine of these animals was always completely filled with large amounts of food: "The stomach is astonishingly large, its length is 6 feet (180 cm) and width 5 feet (150 cm); it is filled with food and seaweeds to such a degree that four strong men with great difficulty can scarcely drag it from its place with a rope."

The animal's feces "by its form, amount, odor, color as well as all other essential characteristics is recognized by the experienced stable-man as that of a horse". Steller, in his first days on the Island, considered these feces which were thrown up by the sea as horse feces, and considered this as a proof of his view, that America was not far from this place (no horses were present at that time in Kamchatka) (V.H.).

²⁴... One of these animals was stranded on dry land because it slept and the sea at that time receded, so it was not able either to go back or to resist. It was killed with cudgels and axes.





36-37 Fig. 8. Bering Island. The coast on which Steller's sea cow was found.
Photographs by S.V. Marakov.

stood on the anterior part of the boat holding the hook in hand; and when he was able to hit the animal, he did. Thirty persons who were standing on the shore holding the end of the cord tried to hold the animal and with great effort pulled it to the shore; the animal, at that time, resisted with fear. Those who were on the boat, held their place with the help of another rope, and continuously beat and stabbed with knives and other sharp instruments to such a degree that the weakened animal, completely exhausted and worn out by the wounds, was drawn up on the shore.

Some [people] cut large pieces of meat from the animal while it was still living. During this, the animal only struck violently with its tail here and there, and so strongly resisted with its hands that large pieces of the superficial skin layer were usually detached from them. Moreover, the animal was deeply breathing and moaning. Blood shot upwards as a fountain from the wounded back; so long as the head of the animal was hidden in water, there was no bleeding, and when it took a breath in air (for this reason it raised its head from water) bleeding began



Fig. 9. Peregrebnaya Bay near Cape Manati on Bering Island—the former habitat of Steller's sea cow. Photograph by S.V. Marakov.

again. This is because when the back was wounded, the lungs which lie under it were also wounded and the more frequently the lungs were refilled with air, the more frequently they expelled blood . . .

The adult and very large animals are more easily hunted than calves, because the latter swim more rapidly and vigorously. If a harpoon was thrust in them [large ones] and was firmly attached to them, it remained in their bodies and was held there, but the calves sloughed off their skin and escaped, as was observed many times.

- 40 If the harpooned and captured animal begins to struggle strongly, only the animals in the herd swimming nearby come close to it and try to help it. Thereupon some animals try to turn the boat upside down with their backs, while others lie on the rope²⁵ and try to cut it off or to strike the rope with their tails to pull the harpoon out of the back of the injured animal, and this they sometimes succeeded in achieving. Definite proof of their abilities and at the same time, of their conjugal love was shown in that one male whose female was captured by a harpoon and pulled out onto the sea shore, tried with all his strength to help her, but his attempts were unsuccessful, and in spite of all the blows which we dealt him, he followed the female to the shore, and several times suddenly threw himself like an arrow toward her although she was already dead. The next day, as we were getting ready early in the morning to cut the dead animal into pieces, we found the male still standing beside his female. Even on the third day, when I came to investigate the internal organs in detail, the male was still there.

Concerning its voice, this animal is dumb and does not produce any sound. It only breathes loudly and also moans when wounded. But concerning sight and hearing, nothing can be said. These animals always hold their heads under water and therefore they cannot hear or see well. This gives the impression that the animal itself has no need for these senses.

. . . Several times it occurred that dead animals were cast up by storms around Cape Kronotskii, which is called the Nose, and Avacha Bay [on Kamchatka]. Because of the type of food which is consumed by these animals, the inhabitants of Kamchatka called these animals "Kapustnik" [cabbage-worm] in their language, which means eaters of weeds; I learned of this, when I returned (from Bering Island, V.H.) in 1742.

²⁵According to the description of Bering's companion, Sofron Khitrov, rope of 4.5 inch diameter, i.e. about 100–110 mm was employed (Pekarskii, 1869).

. . . The fat layer under the upper skin layer and the dermis covering the whole body is as thick as a palm's width, and in some places, three-quarters of its width. The fat is full of glands (!), soft, white in color, but in sunlight it turns yellow, like May oil. The odor and taste of the fat is pleasant and cannot be compared with that of any other marine animals, and it even exceeds that of tetrapod animals. Moreover, this fat can be kept for a long time even on very hot days, for it neither spoils nor smells. After melting it is delicious and tasty, and is preferred to any other oil. Its taste is almost like sweet almond oil and it can be used for any purpose for which any oil is used. It burns brightly in lamps and produces no smoke or bad smell. . . The fat of the tail is harder, stiffer and therefore it is more delicious when cooked. The meat has stiffer and thicker fibers than beef; it is also redder in color than meat of terrestrial animals and it is surprising that the meat of this animal can be kept in the very hot days for a long time without producing any smell, even if it is everywhere full of maggots[. . .]²⁶

The meat of this animal, it is true, requires a longer time for cooking but when cooked, it has a superior taste and cannot be differentiated from beef. The fat of young sea cows is similar to that of fresh swine lard and it is hardly differentiated from the latter. Moreover, their meat cannot be differentiated at all from veal, and it also is cooked rapidly; during cooking, it also swells like young pork meat and occupies in the pot twice the space as originally.

41 Fat in deposits, as in the head and tail, is viscid and therefore can scarcely be boiled. The most preferred muscles are those of the lower surface of the abdomen, back and flanks. Such tallow is not only fit for salting—which many persons doubted—but when salted it is like that of corned beef and has a very nice taste. Internal organs—heart, liver and kidneys—are very hard and we did not utilize them because we had enough meat, for a mature animal weighs nearly eight thousand pounds which equals eighty centners, or 200 Russian poods (3200 kg). The number of these animals was large on this single island, so the inhabitants of Kamchatka might continuously feed only on them.

A particular harmful insect*, like a louse, causes much trouble to sea cows. They stick in large masses on the wrinkled limbs, on mammary glands, teats, in hidden places, anus and in the shagreen-like

²⁶The explanation given by Steller of this phenomenon is of no interest, but the fact itself of the possible long-distance transport of bodies by the sea, especially to Kamchatka, is significant (V.H.).

*See footnote 19, p. 24.—Sci. Ed.

cavities of the upper skin layer. . . . These insects pierce both the upper layer of the skin and the dermis and protuberances are formed from the released fluid, and here and there visible warts. However, these insects are pursued by the sea-gulls which sit on the back of the animal and pick them up daintily. Thus they offer a pleasant service to the animals which suffer from these harmful insects . . .”.

Geographic Distribution and History of Extinction

Steller discovered the kapustnik in 1741 on Bering Island. Later, it was established that this animal lived also on Mednyi [Copper] Island, but information about this is very scanty. In the historical period, sea cows were not found anywhere else. The sea cow is completely analogous to Steller's [Pallas's] cormorant (*Phalacrocorax perspicillatus* Pall.), which was also limited, apparently, in its distribution to the Commander Islands and also was exterminated somewhat later—in the middle of the nineteenth century.

It seemed that the sea cow must have been living in the Aleutian Islands, where the living conditions are actually the same as in the Commander Islands. The standing crop of sea weed is also great there, and the same species grow as in the Commander Islands; generally, they comprise one geographical and zoogeographical region. This particularly applies to Attu Island, the most westerly of the Aleutians (Blizhniye group) and the nearest one to the Commander group (about 350 km from Mednyi Island).

Moreover, Steller did not refer to this species in places east of Bering Island in any of his works, including the diaries, that were published by Pallas (1793) after his death. There is also no record in the descriptions of any other voyages in the eighteenth century. As a result of a special collection of information and complete analysis of the question of the geographic distribution of this species, [von] Baer (1838)* noted the complete absence of this animal at any time in Russian America, including the Aleutian Islands, especially the Lis'ie and Andreyanov islands.

Later, Stejneger (1883), in his evaluation of all information (testimony of Aleuts from Attu, data on Semitki and Agattu islands, as well as observations of Turner, Voznesenskii and others), denied the arguments, which are actually very vague, concerning the existence of Steller's sea cow on the western Aleutian Islands including Attu.

*Actually published in 1840—D.D.

He denies the existence of sea cows on Attu and [the report of] Nordenskiöld (1882), based as it was on unwarranted dependence on testimony of inhabitants. A single rib found on Attu by Voznesenskii, if it actually belongs to this species, came from the body of a dead animal cast up by waves,²⁷ as Brandt (1846) correctly concluded.

In American literature, including the latest (Murie, 1959; R. Rausch, 1960), there is no evidence of the occurrence of Steller's sea cow
 42 around Alaska or on the Aleutian Islands, or any discovery of its remains (not taking into account the case given by Voznesenskii). There are neither archeological nor paleontological remains of this species in the American territories (information from Ch.A. Repenning, paleontologist, U.S. Geological Survey; only known are the remains of a closely related genus *Halianassa*, which is not younger than middle Pliocene, from the eastern part of the Pacific Ocean). In fact, if we leave aside possible historical causes, it is very difficult to imagine the emigration of a herbivorous animal which is so closely associated with the seashore and which has very little vagility, across 350 km of open ocean from Mednyi to Attu islands.

Sea cows were never seen in Kamchatka and were generally absent on the Asiatic shores. Neither Steller (1751, 1753, 1781, 1793) nor Krasheninnikov (1755) made any reference to such an occurrence. All of Krasheninnikov's information (1755) was related to Commander [Bering] Island and, as mentioned above, was based on Steller's manuscripts, which were at his disposal. There is direct information about the absence of this species in Kamchatka in the eighteenth century. The situation wherein some inhabitants of Kamchatka knew about this animal which they called *kapustnik* ("cabbage-worm") is explained by the washing up of bodies (see footnote on p. 40) and finding in their stomach after dissection of a large mass of "sea cabbage", as was correctly noted by Stejneger (1883) (see footnote on p. 35; field cabbage was not known at that time in Kamchatka). The distance from the nearest point on Kamchatka (Cape Kamchatka) to Bering Island is 150 km, a distance across which a carcass could be transported but certainly insurmountable for a living animal. The absence of sea cows along the Asian coast was emphasized by [von] Baer (1838), who showed especially that this animal was absent not only in Kamchatka but also in the Kuril Islands.

Later, Ditmar (1900) referred to the absence of sea cows on Kamchatka in his 1852 material. Finally, it is known that in the middle

²⁷This rib could have been brought by workers who were preparing meat in the Commander Islands (V.H.).



Fig. 10. Tundra Bay on Bering Island—a place where sea cows occurred.
Photograph by S.V. Marakov.

of the eighteenth century, commercial expeditions to the Aleutian Islands and Alaska, for trade in beavers, [sea otters] and other fur-bearers, stopped off especially at Commander [Bering] Island to prepare sea
 43 cow meat and even wintered on the islands for this purpose. This was done because this animal was not found on Kamchatka (Pekarskii, 1869; Ditmar, 1900 and others; see below).

Some reports of the presence of sea cows on the Asiatic coast are found in the literature, but they are false. Thus, the reports of the observation (1762) of sea cows at Cape Shelagskii and between it and the Kolyma, in the ice of the East Siberian Sea (Grekov, 1958, from a document of Shalaurov), were based on some strange misunderstanding. Such a casual remark as Nordenskiöld's (1882)* in which he says that "one Russian", around 1910, saw a dead sea cow supposedly washed up by the sea at Cape Chaplin (north of 64° N. Lat.) is not trustworthy. Finally, in the light of what has been said above, and as all the data on the biology of the sea cow make absolutely clear, "observations" of this species at Cape Navarin in the Bering Sea (about

*Actually attributable to Sverdrup (1930)—D.D.

62° N. Lat.) in 1962 (Berzin, Tikhomirov, Troinin, 1963) have no value at all (Heptner, 1965, see below).

The history of the extinction of the sea cows is considered the most tragic history of the destruction of a most remarkable animal in a very short period, and at a time when the technology of animal destruction was at a low level. Steller's sea cows were in the true sense of the word eaten up by human beings.

As is clear from Steller's description and from other information (see below), the meat and fat of sea cows were characterized by their excellent quality. This fact was sufficiently widely advertised by Steller, who returned to Kamchatka in autumn 1742. Moreover, he suggested—that this probably was a mistake—that the number of sea cows around the island was very large. In fact, these animals were, apparently, numerous only where the crew of the "Saint Peter" was shipwrecked and spent the winter, and in some other especially favorable parts of the coast. The total number of these animals could hardly have exceeded some hundreds.

What is then the cause for such intensive destruction of this animal, which lived around the shores of two similar, small islands lying far out in the ocean, and which had been just discovered and were uninhabited? On the one hand, Steller wrote diligently about the quality of the meat and fat of the sea cow, and especially about the fact that Kamchatka at that time could not supply with foodstuffs the numerous commercial ships which were sailing from Petropavlovsk and Bol'sheretsk in Kamchatka to the east and northeast. The Commander Islands therefore became a base for obtaining provisions for the crews of these ships. The system of hunting was constructed surprisingly rapidly and its organization was very flexible, and the "profusion" of the island was rapidly appropriated. In the next year after Steller's return, i.e. in 1743, the ships which were sailing to trade in the Aleutian Islands and in Russian America went at first to Bering ("Komandor") Island and worked there preparing sea cow meat, overwintering because of this. Later this was continued by all the numerous commercial ships directed from Kamchatka to the east for hunting arctic foxes, fur seals and, above all, Kamchatka beavers [sea otters].

The Marine Department in Petersburg in 1765, apparently in questioning the merchant Vasilii Shilov about the distant lands situated beyond the Commander Islands, and about the trade and geographical discoveries conducted there by the commercial companies, asked him particularly about the "means" that they had in those far and long

voyages “. . . how you were saved from hunger, because the food prepared in Kamchatka was for two or three months, and flour was especially insufficient?” The answer declared that the “trading companies at present are far from Kamchatka beyond Commander and Mednyi and near to the North, and of others, several islands became better known far to the East”, however, Kamchatka “cannot provide such distant routes with provisions, especially for prolonged residence there
 44 for hunting, and thus they used, except for flour, the abundance of Commander and Mednyi islands”. From Kamchatka, the ships took besides flour, only such provisions and fresh water as helped them, even in unfavorable weather, to reach the Commander Islands “. . . and there they spend the winter; and during the whole wintertime they are engaged in hunting, and on the distant routes they prepare provisions which mainly consisted of sea cows, whose meat is not only wholesome and in great quantities, but can also be used instead of bread when dried. In this animal there is much fat to be stocked in small barrels and used in meals instead of oil, and one can drink it harmlessly like the best [olive] oil. It can also be used for making fire instead of candles. The skin of these sea cows is used instead of boards in the planking of boats . . .” (Pekarskii, 1869).

Hunting itself was, on the whole, performed in the same way as that of the people on Bering Island, and it was based on the same biological characters of the animals, i.e., on their habit of coming to the shallowest water at ebb tide. However, some changes appeared in the technique. Peter Yakovlev describes it in the Nizovtsovaya harbor, where “. . . in the sea, near the shore, these sea cows were seen singly or in groups. In hunting they go in a boat, eight in a group, of which one hunter stays near the stern in front of the helmsman holding a long pole armed with a wide, long sword-like band (called “pokolyuga”), and the rest of the hunters sit as oarsmen. When they find themselves in front of a sea cow’s head, they turn the boat with the stern towards the sea cow and the hunter with the “pokolyuga” inflicts a severe wound in that beast’s heart. After that the rowers must row quickly away from the sea cow in order to get out of that wounded sea cow’s reach, for it can ruin their boat by its tail or fluke . . . with such a wound in its heart, the cow does not swim in the sea for a long time. It soon gets tired, stops and turns with its belly up. The hunters pull that sea cow by a hook [harpoon, V.H.] towards their boat, tie it to the stern of the boat and row to the shore. The meat of one sea cow was enough

for 33 men for a month. The net weight of one sea cow's meat and fat, without bones, reached 200 poods²⁸ (Pekarskii, 1867).

Moreover, as Vasilii Shilov describes, workers used the skins of sea cows in covering the frameworks of boats instead of covering them with wooden boards. From Kamchatka, they took "the ready-made wooden boat keels and the stern and bow installations for one or two boats" and covered them with sea cows' skins in the Commander Islands, "because" he notes, "such large skins are not present in Kamchatka" (this also proves the absence of the above-mentioned species on the continent). Sewn skins (that is, from animals of smaller size) are not convenient because they leak.

Shilov further stated that "though the ship-chandlers take with them all the prefabricated parts, until they are actually needed (almost, V.H.) they do not cover them with the skins but prepare *excess skins* (my emphasis, V.H.). Nevertheless, they store up skins in a great quantity and when necessary they gathered the boats in a short time, and covered them with skins after soaking them in water . . ." These skins were, apparently, of a great value because the boats were safer in the breakers, and what is more important, they were comfortable in handling and very light in comparison to wood-planked ones. "A boat covered with leather carried the same number of people (as a wood-
45 planked one—20 men, V.H.) and it could be pulled out onto the shore or from the breakers, like a bladder, without risk, and could be carried a good distance by only four men. . . ."

As shown, Steller's sea cow was used by pioneers in developing Kamchatka and Russian America rather fully, but too excessively. As a result, it was quickly exterminated and in 1768, that is only 27 years after its discovery, the last one was killed on Bering Island. The animals around Mednyi Island, which were, undoubtedly, fewer, were exterminated earlier; at any rate, in 1754 there was not a single one of them.²⁹ It is possible that on Mednyi Island one or two outlived the indicated date for a year or two; however, in the seventieth decade of the eighteenth century nobody saw them and Bragin, who was spending the winter on Bering Island in 1773–1774, makes no mention of sea cows. There are no later records of them (Berg, 1946).

²⁸Steller (see above) apparently considered that 200 poods is the total weight of the beast (V.H.).

²⁹Peter Yakovlev, sent by the government according to the suggestion of M.V. Lomonosov, to Mednyi Island to search for useful minerals (copper), whose whole

The rapid extermination of sea cows was caused by thoughtless, rapacious forms of exploitation which led to the unjustified annihilation of a great number of animals. As seen from the descriptions of the methods of hunting, success was only ensured in cases where many people at once (not less than 20) were hunting one animal. Attempts to get an animal by a small group of hunters were often useless. The above-mentioned P. Yakovlev writes of this as follows: “. . . those hunters live in yurts or winter houses in different places along the northern shore of the Commander Islands in groups of 2 and 3 hunters and they hunt for arctic foxes and other marine animals. They do not have any other food except the meat of [sea] cows; the herds of cows live in the sea near the shore and are frequently wounded by people, but those wounded cows swim out to the sea and there become further weakened by their wounds. They are later washed ashore after a long period of time when their meat becomes bad and inedible.

By this sort of hunting sea cows are eradicated, and *although many are slaughtered* (my emphasis, V.H.), not a single fresh sea cow comes to their hand, and the hunters therefore suffered from starvation, and the sea cows were exterminated.” Yakovlev foresaw the quick extermination of the sea cows on Bering Island and tried to take measures for the protection and wise use of the stocks of this most important animal at that time. “For this purpose, on his (Yakovlev’s) return from one sea voyage (i.e. sailing to the Commander Islands, V.H.) it was reported on the 27th of November, 1765* to the Nizhne-Kamchatskii Ostrog [fort] that hunting of the sea cows should be prohibited by order (Dokladnaya Zapiska, V.H.) of the Bolsheretsk office in order to save one Commander Island [Bering] from devastation because Mednyi Island had already been devastated . . .” (Pekarskii, 1867). However, as is known, nothing came of Yakovlev’s attempt. In this way, the sea

expedition consisted of 33 persons, could not spend the winter on this island in 1754,** i.e., 13 years after the discovery of sea cows on Bering Island, because sea cows were absent . . . “Mednyi Island was found empty—he wrote—and . . . for the expeditionary force to spend the winter was impossible—due to the absence of sea cows the inhabitants of this island suffered from hunger.” Further, he wrote that “before the sea cows were found in large herds but now these cows were destroyed, so none of them could be seen; and now in the Mednyi Island there is not a single sea cow . . .” (Pekarskii, 1867). Yakovlev and his “command” spent the winter on Bering (“Commander”) Island (see below).

*This date should be 1755, since 13 years later, in 1768, the last one was killed on Bering Island (see previous page)—D.D.

**Misprinted 1745 in Russian original—D.D.

- 46 cow at Mednyi Island was destroyed ten or twelve years after its discovery. After approximately the same period, they stood under threat of extermination at Bering Island, and 13 years following Yakovlev's attempt to protect this animal, was also completely destroyed there.*

All information about the existence of the sea cow, which occasionally appeared in the literature at the end of the eighteenth and the beginning of the nineteenth century, as was shown by K. [von] Baer (1838) and J.F. Brandt (1846), cannot be credited. Separate information appeared later concerning some of these animals (for some, see Grekov, 1958). The most famous of such reports, which seems most plausible, is that of Nordenskiöld (1882), in which it was mentioned that a sea cow was observed on Bering Island in 1854. As was explained by Stejneger (1883, 1885), who interviewed the same people to whom Nordenskiöld referred, this information was found to be false. Stejneger (1883) suggested that these animals were whales of smaller size or, probably, female narwhals, which very rarely passed so far to the south and therefore were considered unusual for the Aleutians. Some other unreliable and unconfirmed information is not likely at all and is not worth discussing. Some of it is simply fantastic (observations in . . . California!).

Even the slightest probability is lacking in the latest information given by Berzin, Tikhomirov and Troinin (1963), on the observation of a sea cow in July 1962 at Cape Navarin (!), i.e. somewhat north of 62° N. Lat. This information contradicts all the known facts about this species, which are partially given above. It was based on complete ignorance of the question and its literature (even the new literature), on the biology of the animal, characteristics of its habitat, and its behavior as well as the history of discovery and exploitation of northeastern Siberia and Russian America in the eighteenth and nineteenth centuries. This was actually the result of naive pursuit of sensation.

Still, in our time, remains of sea cows are sometimes found. These remains have become rare, although a skull was found in the decade of the 30's and two lower jaws in a well-preserved condition were collected in 1960 (N.N. Kartashev, Zoological Museum of Moscow University).

There are, in general, numerous bones and skeletons of sea cows preserved in museums of our country and in foreign museums which

*See foot note on previous page—Sci. Ed.

were collected from the Commander Islands. It is interesting that at the beginning of the last century, a masticating plate was the only material at the disposal of [von] Baer, and Brandt (1846) had only one imperfect skull. At the beginning of the 80's, Stejneger (1883) collected more than 11 skulls and believed that more skulls could be collected. B. Dybovskii brought some specimens from the Commanders in those years. Now, such collections are impossible* (V.H.).

*Specimens have been collected as recently as 1992—D.D.

ORDER OF CARNIVORES

Ordo CARNIVORA Bowdich, 1821

Superorder of Carnivores
Superordo FERAЕ Linnaeus, 1758

Order of Carnivores

Ordo CARNIVORA Bowdich, 1821

- 49 The order includes species of relatively generalized type and clearly, sometimes very sharply, specialized ones. A few are large, the majority are of middle and small size, while some are of very small size. They are typically terrestrial animals, in few cases, semiaquatic, and as an exception aquatic animals of various construction and appearance, from heavy and clumsy animals to light, slender and very mobile. The tail is usually long (about half the body length or more), rarely short, of approximately the length of the hind foot.

The extremities are plantigrade, semidigitigrade or digitigrade, digits are usually 5, but in some one is absent. Digits are provided with claws, in some species retractile; the terminal phalanges are not flattened and not widened, but always laterally compressed. One digit is never opposed to the others. In the wrist, the scaphoid (scaphoideum), semilunar (lunatum) and central (centrale) bones are fused. The articulating surface of the astragalus is pressed inward. The ulna and fibula are normally developed and separate (not fused).* The foramen entepicondyloideum on the humerus is either developed or absent; the third trochanter of the femur is absent. The clavicle is either absent or rudimentary.

There are no more than 22 lumbothoracic vertebrae, usually 13 thoracic, and 7 lumbar. The vertebral column is, in the majority of cases, very flexible. The number of caudal vertebrae varies greatly.

The form of the skull is extremely varied—in some animals it is elongated with highly developed facial part and a relatively short cranial one, while in others the skull is very short, with rounded outline and with relatively large and voluminous cranium. All the transitional forms are also present. The hard palate is continuous, the eye socket is usually open, and only exceptionally superficially separated, but in the

*Sic; refers to radius-ulna and tibia-fibula being distinct bones — Sci Ed.

majority, it communicates widely with the temporal fossa. The eye sockets are directed forward and in several, strongly approximate (binocular vision). The tympanic bulla (with one exception—*Nandinia*) is ossified. The wing-shaped (ectopterygoid) fossa (f. pterygoidea, s. ectopterygoidea) is not manifested in the majority of cases due to the absence of the corresponding independent process of alisphenoid.

50 In the greater number of species, the crests and zygomatic arches are strong and widely separated, a fact associated with the great development of the jaw musculature. Ethmoturbinal (ecto- and endoturbinals) olfactory folds are 5–7; the maxilloturbinal has double flexures or branching. The articular condyle of the lower jaw is semi-cylindrical and the glenoid fossa on the skull is elongated, occupying a transverse position. It is usually more or less deep, sometimes so much so that its anterior and posterior edges tightly envelop the condyle of the lower jaw. The angular process of the lower jaw is small and with no inward flexure.

The dental system is heterodont and diphyodont. The complete

formula is $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{4}{4} = 48$, but usually the teeth are much fewer.

The reduction occurs at the expense of the cheek teeth and mainly at the expense of the posterior molars and (to a lesser degree) of the anterior premolars. The number of incisors is only rarely reduced to

$\frac{3}{2}$ (Kamchatka “beaver” or sea otter,* *Enhydra*) or to $\frac{2}{3}$ (sloth bear,

Melursus). The minimum dental formula is $I \frac{3}{3} C \frac{1}{1} P \frac{2}{2} M \frac{1}{1} = 28$ (manul,

Felis manul) and even $I \frac{3}{3} C \frac{1}{1} P \frac{1}{2} M \frac{1}{1} = 26$ (fossil sabre-tooth tiger,

Smilodon, of Machairodontinae).

In one case (bat-eared fox,** *Otocyon*) the dental formula may be

$I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{3-4}{4-5} = 46 - 48 - 50$.¹

*In Russian, *Kalan*—Sci. Ed.

**In Russian, long-eared fox—Sci. Ed.

¹The greatest number among recent placentals. Probably, this increase is a secondary character and is connected with the transition to a considerable extent to entomophagy (mainly grasshoppers).

The teeth always are rooted, brachyodont, cusped-cutting (tuberculo-sectorial), quadri- or multituberculate with sharp, or rarely blunt, apices. The teeth are strongly differentiated. Incisors are small and the canine is usually strongly developed. The fourth upper premolar and the first lower molar are usually large, with sharp cutting apices ("carnassial teeth"), rarely with a more or less flat, bluntly tuberculated, masticatory surface. A true diastema is absent.

The stomach is simple; the caecum is normally or weakly developed or absent. The brain is macrosmotic, the hemispheres are large with three suprasylvian fissures. The pelage is always well developed, composed of different hair categories (underfur, guard hair, directional hairs), sometimes very dense, relatively long and fluffy, and sometimes sparse and rough. The tail is usually fluffy. Vibrissae are well developed. The color varies greatly, being more or less monotone, or light with bands, spots, shabrak*, etc.; some species are polymorphic. The skin glands, with some exceptions, are normally developed; the majority of glandular complexes and large, complicated, often odiferous glands (musky stink glands of skunks, etc.) develop in the anal region in connection with the male genitalia. The milk glands—inguinal and abdominal—range from 6–7 to 2 and one pairs. The scrotum is well developed or else the testes are located subintegumentarily, but always outside the abdominal cavity ("extra-abdominal"), and behind the copulatory organ. In the latter (except in hyena) a bone (os penis, baculum**) is present. The uterus is doubled or with 2 horns. The placenta is deciduous and zonal².

Sexual dimorphism is absent or weakly manifested except in the general size of the species with rare exceptions (lion). Age dimorphism in some species is quite significant (wolf, lion and others), while in the
 51 rest it is not manifested. Seasonal dimorphism, mainly in the density and length of fur in the forms of temperate and northern latitudes, is quite great and sometimes connected with changes in color, in which case it is sharp (arctic fox, ermine), while in the others it is weak or absent. In the forms of temperate and cold latitudes that are active in winter, there are two molts which usually occur rapidly. In species of those districts which spend the winter sleeping, the single molt extends

*Lit., goatskin; refers to a goatskin saddlecloth, hence by extension, to a "saddle" pattern on the back—Sci. Ed.

**Spelled *baculum* in Russian original—Sci. Ed.

²Occasional reference to the placenta as of the discoid type (for example, Novikov, 1956) is a mistake. This was, apparently, based on a slip of pen in the diagnosis of the order by Weber (1928).

over almost the whole summer (the summer fur is considered a transient coat). In warm countries, there is usually one molt.

Carnivores differ greatly in size—the largest has a head-body length (excluding tail) to 300 cm and a weight to 725 kg and even 1 metric ton (polar bear). The smallest form—the least weasel (*Mustela nivalis pygmaea*) has a body length of 115–140 mm and a weight of about 100 g; i.e. the smallest weight is less than the greatest one by about 10,000 times (in case of artiodactyls this proportion is about 1 : 1,150).

In general constitution, proportions and external appearance, biological types, adaptation forms and other characteristics, the carnivores are one of the most variable if not the most variable, of the orders of mammals, including forms that are comparatively generalized types (some bears) as well as extremely specialized ones (Kamchatka beaver, or sea otter).

Among the carnivores there are heavy animals of low mobility and slow movement (bears) as well as light and slender, rapid and swift runners (wolf, cheetah), excellent swimming forms closely connected with water (otters) and excellent climbers, and even partially specialized arboreal animals (some martens, viverrids and cats); some are excellent diggers (badger), etc. Carnivores inhabit all latitudes, landscapes and the vertical montane belts. They live individually or in pairs, and some are found in small packs (wolves, hunting dogs) at least in part of the year. The majority are sedentary and are fairly strictly restricted to their hunting areas; others wander widely, while several accomplish regular seasonal migrations.

Some species are associated the entire year with holes (badger); others, only in some parts of the year (time of reproduction) and a third group has only open lairs even in the lactation period. Some are associated continuously, or only at the time of reproduction, with tree hollows, rock clefts, caverns and other similar shelters. Several species of cold and temperate latitudes hibernate in winter. A series of species are monogamous and live in pairs for more than one reproductive season, while others form pairs only for one cycle and in others, the male does not take any part in provisioning the young at all. True polygamy (in the form of a "harem") does not occur.

The young range from 1–2 to 13 and even 20–22.³ However, the number of young in the litter varies strongly within one species. The

³Maximal known number is in the wolf (13) and in arctic fox (22). Normally, these numbers are much less.

offspring are born helpless, blind with closed ear openings and undivided fingers, etc. and they develop and grow comparatively slowly.

Carnivores are extremely variable in their food habits. The majority are sarcophagous, at times very narrowly specialized, feeding on the meat of mammals and birds, and rarely ichthyophagous and polyphagous, in the diets of which a significant role is played by lower vertebrates, terrestrial and aquatic (mainly fresh water) invertebrates and plants. The number of species that are chiefly plant-eaters (phytophages) is few; specialized entomophages comprise exceptions, (aardwolf*—*Proteles*).

Among the sense organs, smell and hearing are well developed, sight is usually weak, and not color. The external ear pinnae are very different in size, from equal to head length (fennec) to almost undeveloped (otter).

53 Carnivores are very widely distributed, occupying nearly the whole world. Aboriginal species are absent only in Australia and in some islands and island groups. In the north, they are met with in the northernmost islands (New Siberian, Severnaya Zemlya, Franz Joseph Land, Arctic archipelago of [North] America, Greenland) and even in the ice of the Arctic Ocean, considerably to the north of these islands, all the way to the pole (polar bear, arctic fox). The species of other orders, even the pinnipeds, do not penetrate so far north. Carnivores are absent on the island of the West Indies and the other islands of the Atlantic, except for Newfoundland, Iceland and Jan Mayen. They are also absent, with the exception of the Falklands, on the islands of the southern oceans, small islands of the Indian Ocean, in Tasmania, New Zealand and New Guinea, Vetar [Wetar] and Ombai, in the Lesser Sundas (on others, including Timor in the east, they are present), Tenimber [Tanimbar], Kei and the majority of the Moluccas (except for Halmahera, Buru and Ceram), in the Talaut [Talaud] archipelago and on all the islands which lie to the east of New Guinea and on the Hawaiian and Galapagos Islands. They are found in Ara, Sulawesi (Celebes), Philippines, Ryukyu, Kuril, Sakhalin, Commander, Aleutian and Pribilof islands.

The geographic range of the order has not essentially been changed since historical time and it was not reduced—with some exceptions [extirpation of the Falkland “wolf”, *Canis (Dusicyon) australis* = *antarcticus*]. The geographic range was artificially widened for some

*In Russian original, maned “wolf”—Sci. Ed.

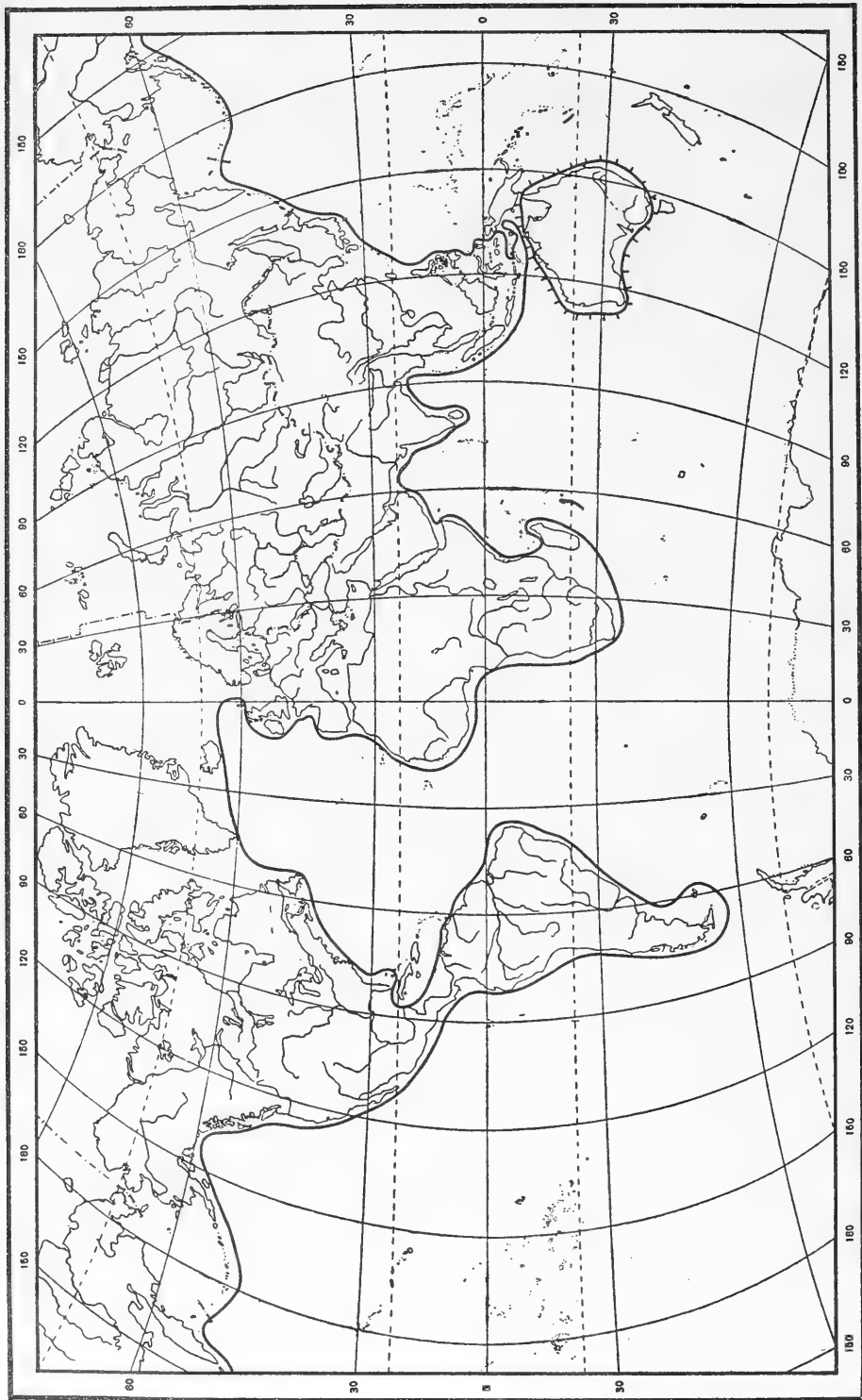


Fig. 11. Geographic range of the terrestrial predators, *Carnivora* (reconstructed). The line surrounding Australia denotes the range of the dingo (*Canis dingo*). On the islands of West Indies lives the acclimatized mongoose, *Herpestes javanicus auropunctatus* Hodges, V.G. Heptner.

species; the Indian mongoose was established in some islands of the West Indies, Fiji islands and several others; the European red fox was introduced into Australia, etc. The dingo ("*Canis familiaris dingo*"), occupying the entire continent of Australia, is not an aboriginal species. This is a feral dog, which was introduced into Australia a very long time ago by the ancestors of the contemporary Australians as a domestic animal.⁴

On account of the diversity of biological types and forms of specialization which allow carnivores to occupy almost all habitable media, the breadth of their geographic distribution, the diversity and abundance of species, the relatively high numbers of many of them, and other characters, carnivores without doubt may be considered a flourishing and quite recent group. Although anthropological factors have negatively influenced a series of species, decreasing their geographic ranges and numbers, this influence is, however, generally less in relation to this order than if compared to several others. The "resistance" of carnivores to this very strong destructive factor is an indication of their vitality.

Concerning systematic relationships, carnivores are closely related to pinnipeds (Pinnipedia). The latter are considered to be derived directly from carnivores comparatively recently (Oligocene). All their characteristics have been formed as sharp and direct progressive adaptations to an aquatic (marine) way of life. Some more primitive recent pinnipeds (Otariidae—eared seals) are, in their least specialized characters (skull), very similar to the generalized forms of Carnivora (Steller's sea lion,* *Eumetopias*). Many authors unite carnivores and pinnipeds in a single order Carnivora, dividing both groups only into the rank of suborders: Fissipedia and Pinnipedia. Such a view was mainly based on paleontological data. The alignment of the recent groups (by the "horizontal" system), however, is such that for the purpose of keeping with the sequence in the mammalian system, it is more natural to consider Carnivora and Pinnipedia as separate orders.⁵

⁴The origin of the dingo from the primitive dogs of the tropical zone (Shensi type "*Canis familiaris schensi*") is indicated by the fact that the species of the genus *Canis* are absent in the Malayan archipelago, and they (wolves and jackals) begin to occur only in Indo-China and India.

*In Russian, *sivuch*—Sci. Ed.

⁵Accordingly, in this edition, the suborder Fissipedia is opposed, not to the suborder Pinnipedia, but to the suborder Creodonta. In Simpson's system (1945), Creodonta, Fissipedia and Pinnipedia are considered as suborders of the order Carnivora.

54 The features that approximate carnivores with insectivores are relatively great, and those which link them with artiodactyls and perissodactyls are strongly divergent, and essentially in a purely historical relationship (see vol. I). Their relationship with whales, which is frequently emphasized and sometimes regarded as very close, is apparently not more close than the relationship to ungulates.

The ancient and most primitive group of Carnivora—Creodonta—has a great phylogenetic significance. They stand at the root of the extensive cohort Ferungulata, comprising the orders of pinnipeds (Pinnipedia), tubulidentates (Tubulidentata), proboscideans (Proboscidea), hyraxes (Hyracoidea), sirenians (Sirenia), even- and odd-toed ungulates (Artiodactyla, Perissodactyla) (see p. xx).

Carnivora is one of the most ancient orders of recent mammals, stemming indirectly from the insectivores, the most primitive and ancient placentals. The primitive carnivores, the lower Creodonta (Arctocyonidae), appear in lower Paleocene (North America) and are represented by forms which are intimately connected—in certain respects “transitional”—with primitive Cretaceous insectivores (Insectivora). Creodonts lived through their flowering in the Eocene and were still relatively well, but notably less richly developed, in the Oligocene. Their last representatives (Hyaenodontinae) survived only to the very beginning of the Miocene. True Creodonta were represented by several families (Arctocyonidae, Mesonychidae, Oxyaenidae, Hyaenodontidae) which did not leave any trace. On the same level with these families of the typical creodonts, the family Miacidae existed from the middle Paleocene (became extinct in the Eocene), which by general agreement, was the beginning of modern carnivores (Fissipedia). The unique features of this family—which are, to a certain extent, of “intermediate” character between Creodonta and Fissipedia—gave some authors the basis for considering them among the Creodonta and gave others the basis to relate them to the existing Carnivora and to ally them to viverrids (Viverridae), or sometimes to cats (Felidae) or to wolves (Canidae). If the Miacidae are considered among the existing carnivores (Fissipedia), then the origin of this latter group (from the primitive Creodonta) must be dated to the middle Paleocene. The remaining (recent) families of true carnivores (Fissipedia) appear not earlier than the upper Eocene and the lower Oligocene.

Among the sum of characters, the contrast between the extinct and recent groups of carnivores is relatively small, although in the extinct, even a separate suborder is recognized (see below). It is less than, for

example, in the “ungulate” group. The diversity of the group in the past was similarly not greater than in the more recent (and present) time. The same applies to the general number of species in different preceding epochs. Therefore, in its historical aspects there is basis for considering the order of carnivores as an existing flourishing group.

Classification of the order of carnivores, in spite of the abundance and diversity of species, is, in its main features, simple and does not result in any serious disagreements. Two suborders are admitted—the extinct Creodonta with four families (see above) and the recent Fissipedia. The latter is divided into three superfamilies: the extinct Miacoidae with one family, Miacidae; the recent Canoidea (Arctoidea auct.) with four families—Canidae (wolves), Ursidae (bears), Procyonidae (raccoons), Mustelidae (martens) and the recent Feloidea (Aeluroidea, Herpestoidae auct.) with three families—Viverridae (viverids), Hyaenidae (hyaenas), Felidae (cats).⁶

- 55 Canoidea are characterized by the following characters. Tympanicum formed by the whole outer wall of auditory bulla. Partitions of internal cavity of auditory bulla derived from cartilagenous precursors, or precursors of the tympanicum. Canalis caroticus long. Maxilloturbinalia large and branching, and partition off the nasoturbinalia and ethmoturbinalia from the external nasal openings. Cowper's glands absent. Os penis large.

Feloidea are characterized by the following characters. Tympanicum is, to some degree or other, semicircular and forms only the anterior outer (tympanic) part of the auditory bulla, while the posterior inner part is formed by the entotympanicum (os bullae). The tympanal-entotympanal partition extends deep inside the bulla at the place of divergence of both bones. Canalis caroticus short or absent. Maxilloturbinalia small, doubly flexed, and do not partition off the nasoturbinalia and ethmoturbinalia, which, in this way, approach the external opening of the nasal passage. Cowper's glands present. Os penis small or absent.

Canoidea and Feloidea are sometimes considered to be suborders.

The systematics of carnivores is insufficiently worked out as regards the genera and species. In particular, there is a strong tendency

⁶Attempts were often made to divide some families into several. Among Procyonidae in particular, the [lesser] panda (*Ailurus*—Ailuridae) and giant panda* (*Ailuropoda*—Ailuropodidae) were divided into separate monotypic families. These, and also other arrangements, cannot be considered well-founded and are not widely accepted.

*In Russian, bamboo bear—Sci. Ed.

here towards narrow interpretation of the genus (especially cats, bears and some others) and species (particularly in America).⁷ According to a more or less moderate opinion (Simpson, 1945), the order comprises 338 genera belonging to 12 families, of which 5 are extinct. Extinct genera number 241; recent—97.⁸

Only a very approximate count can be made concerning the number of the recent species of carnivores at the present moment. Their general number is approximately 240 (probably less), constituting only 8% of all existing mammals. On the average, the genus comprises 2.5 species. The greatest number of species is in the families Viverridae (about 75) and Mustelidae (about 70); in Canidae there are 29, Felidae—about 36, in Procyonidae—about 10, Ursidae—7, and Hyaenidae—4. The greatest number of species live in Africa (about 100) and Eurasia (about 90); in South America—about 50 species, in North America—about 35.⁹

In practical relationships, carnivorous animals are one of the most important groups of mammals. Among them, there are a great number of fur-bearing species, some of the most valuable (sea otter, sable), pests of livestock and hunting enterprises (wolf, raccoon dog, yellow-throated marten), destroyers and regulators of a number of harmful animals (mainly rodent—foxes, some martens, viverrids and others), valuable sport-hunting animals (large species of cats, bears), vectors of some domestic animal and human diseases (rabies), animals giving raw material for perfumes (musk), etc.

Some species have been acclimatized in alien countries as fur-bearing animals (raccoon dogs in European part of the USSR, American raccoon, American mink in the USSR), as destroyers of harmful animals (snakes in the West Indies—mongooses). However, these measures are not widely distributed in the sense of territory and number of species. A series of species, as a result of the excessive utilization in connection with the value of their fur or pursued for the sake of destruction for one
56 or another reason, sometimes very strongly, were reduced in number

⁷Lately, a wider approach to the species and genus concepts has been applied in the systematics of carnivores, and it is well-known to be found in a revisionary stage (see below in characters of families).

⁸The relatively high "index of contemporaneity" of carnivores indicates that contemporary genera constitute a sufficiently large part of the total number of genera—more than 28%.

⁹According to Anthony, 1928; Allen, 1939; Cabrera, 1957–1961; Chasen, 1940; Carter, Hill and Tate, 1945; Anderson, 1946; Ellerman and Morrison-Scott, 1951; Roberts, 1951; Haltenorth and Trense, 1956; Haltenorth, 1958 and other sources.

and distribution (sea otter, lion, tiger, bears, wolf, leopard, puma and others). Some forms are exterminated completely or almost completely (Falkland wolf, Cis-Caucasian leopard, Persian and Atlas lion and others). A series of species find themselves under a complete or partial [protective] ban, and some others are kept in preserves. The hunting of the majority of fur-bearing and sport-hunting animals is regulated. Conservation of carnivores usually gives good results.

Carnivores gave rise to several domestic animals. The most important of these is the dog ("*Canis familiaris*") which is the most ancient of all the domestic animals, derived from the wolf (*Canis lupus*).¹⁰ The domestic cat ("*Felis catus*") is a minor, mainly decorative, domestic animal, obtained as a result of the domestication of *Felis sylvestris libyca*. The white polecat (*Mustela putorius furo*)—the albinistic form of the polecat—is only a semidomestic form from western Europe. In the last decades, a series of species (red fox, *Vulpes vulpes*—melanistic form; Arctic fox, *Alopex lagopus*—normal and "blue" forms; American mink, *Mustela vison*; raccoon, *Procyon lotor*; sable, *Mustela zibellina*, and several others) became the objects of different forms of fur farming, mainly hutch farming, and many different breeds of foxes or minks have been derived.

In the fauna of USSR there are 41 autochthonous and 2 exotic acclimatized species, i.e. about 17% of the species of the order, and about 14% of the species of the USSR fauna. Both superfamilies, 5 out of the 7 families (71%) and if the acclimatized American raccoon is considered, 6 families (85%), and 22 genera out of the 97 existing ones (22.5%) are present in the USSR.¹¹

The geographic range of carnivores in the USSR covers the whole territory of the country and the Soviet sector of Arctic Ocean (they are now exterminated in the southwestern part).

In the USSR, representatives of the order are found in all natural conditions, including extremes of high mountains, deserts and the sea-shore.

In the Soviet Union, carnivores constitute a very important group practically. They include the most valuable fur-bearing animals, some of them represent objects of hunting sports, while certain species play a more or less considerable role as pests of livestock and hunting

¹⁰The presumption of the participation of jackal, i.e. the diphyletic origin of the dog, is to the highest degree improbable and is now entirely rejected.

¹¹The number of genera, also mentioned above, is that given by Simpson (1945). Later in the text, several genera will be discussed in a broader manner.

enterprises, carriers of some diseases, and destroyers and regulators of the numbers of harmful rodents. The hunting of almost all species is regulated (definite times of hunting, licensed trade); some are found under complete or partial protection, while certain species are completely exterminated from the country or from some parts of it (V.H.).

*Key for Identification of Families of the Order of
Carnivores*

(Identification by External Features)

- 1 (6). Five digits on hind foot.
- 2 (3). Tail short (shorter than the hind foot) and hidden in body fur or hardly protrudes from it. Size very large, body length of adult 1.4–2 m or more. Bear family, **Ursidae** (p. 586).
- 3 (2). Tail long (longer than hind foot) and always clearly protruding from the fur. Body length less than 1.2 m.
- 57 4 (5). Tail distinctly bicolored—6–7 dark transverse rings distinct against lighter background. Raccoon family, **Procyonidae**.*
- 5 (4). Tail one color, or terminal part darker than base, but transverse dark rings absent. Marten family, **Mustelidae**.*
- 6 (1). Four digits on hind foot.
- 7 (8). Four digits on fore foot. Along neck and back, high, protruding, shaggy crest of long elastic hairs. Color gray (without reddish brown tones), with black stripes across the trunk. Hyaena family, **Hyaenidae**¹².
- 8 (7). Five digits on fore foot (first located somewhat higher than remainder). High crest along neck and back absent. Color different; if black transverse stripes on trunk, reddish brown tones well-developed.
- 9 (10). Head elongated, with long dog- or fox-like muzzle. Tail always reaches tarsal joint; fluffy, but hairs short at base, thus tail is thinner at base than in middle. Claws not retractile, their tips directed forward and downward, slightly compressed laterally and relatively blunt. Color without distinct spots and transverse stripes. Wolf family, **Canidae** (p. 66).

*Described in Part 1b.

¹²Described in the following volume.

- 10 (9). Head round with short, cat-like muzzle. Tail reaches the tarsal joint, or is shorter, covered with hairs of equal length; at base, not thinner than in middle. Claws retractile, their tips directed forward and upward, strongly compressed laterally, and very sharp. If claws not retractile, then of large size (large dogs) and the color is light with small distinct, irregular black spots. Color with spots or transverse stripes, or unicolorCat family, **Felidae**.¹³

Identification by Skull

- 1 (6). Palatine bones protrude backward behind transverse line between posterior points of last teeth, and less than half [palatine] width lies between these teeth¹⁴ (Fig. 12).
- 2 (3). Four teeth in lower jaw on each side behind canine, five in upper; total number of teeth 34.
.Hyaena family, **Hyaenidae**.¹³
- 3 (2). Dental formula different.
- 4 (5). Three teeth on each side in lower jaw behind canine; 4 or 3 in upper; total number of teeth 28 or 30.
.Cat family, **Felidae**.¹³
- 5 (4). Seven or 6 teeth behind canine in lower jaw, 6 in upper; total number of teeth 42 or 40. . . . Wolf family, **Canidae** (p. 66).
- 6 (1). Palatine bones protrude behind transverse line between posterior points of last teeth; more than half their width lies between these teeth¹⁴ (Fig. 12).
- 7 (8). Size of skull large. Maximum length more than 200 mm. . . .
.Bear family, **Ursidae** (p. 586).
- 8 (9). Size of skull smaller. Maximum length less than 200 mm.
- 9 (10). Six teeth behind canine in upper jaw and 6 in lower; total number of teeth 40 Raccoon family, **Procyonidae**.*
- 58 10 (9). Less than 6 teeth in upper jaw behind canine; 4, 5 or 6 in lower; total number of teeth 38 or less.
.Marten family, **Mustelidae**.* (V.H.).

¹³Described in the following volume.

¹⁴Measurement taken along suture between palatine bones.

*Described in Part 1b.

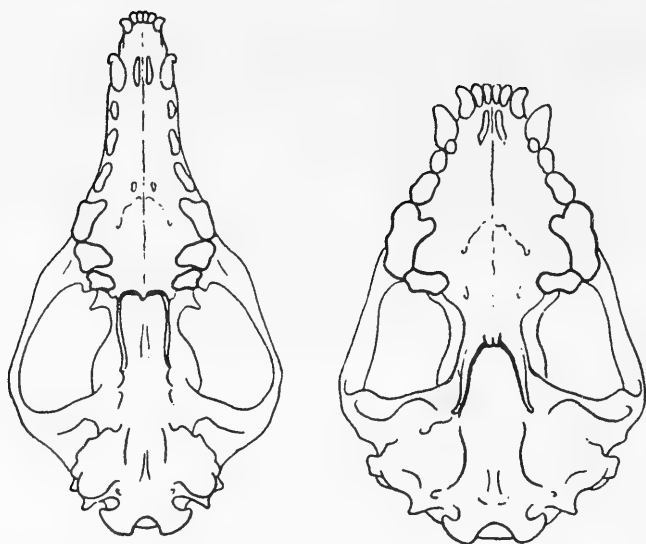


Fig. 12. Skull of fox, *Vulpes vulpes* L., and wolverine *Gulo gulo* L., on right (schematic). Characteristics of palatal construction and relation of the posterior part of tooth row and palate. Sketch by N.N. Kondakov.

Superfamily of Wolves

Superfamilia CANOIDEA Simpson, 1931

Family of Wolves

Familia CANIDAE Gray, 1821

Carnivores of a more or less generalized type, of medium size, with unusually long legs, light, well built and highly mobile.

Digitigrade; tarsal and carpal regions never touch the ground during walking. On the anterior extremities there are five (in one case 4; *Lycaon*) digits, of which I is always rudimentary and located considerably higher than the others; on the posterior extremities, four digits. The two middle digits are considerably longer than the rest. The claws are not retractile, relatively blunt and not sharply compressed laterally. The last phalanges are not capable of flexing far back and upwards and have normal articulating surface.

The skull with long facial portion; small only in exceptional species; swollen auditory bulla, with a more or less horizontal internal partition, and the bone of the auditory meatus is of moderate length. The lateral occipital (paroccipital) process is small, somewhat laterally

compressed, and adheres to the auditory bulla. The mastoid process is small. The alisphenoid canal is well developed.

The dental system is relatively complete; the usual dental formula

is: $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42$. In one species it is $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{1}{2} = 38$

(*Speothos*¹) and in another, it is: $I \frac{3}{4} C \frac{1}{1} P \frac{4}{4} M \frac{3-4}{4-5} = 46-48-50$

(*Otocyon*).

- 59 The carnassial teeth are well developed, whereas the molars are short and quite flat with low blunt cusps; in the upper ones, their width exceeds their length. They have a grinding character, more or less "omnivorous". The canines are highly developed and are sometimes very long and thin.

The caecum is fairly large and spirally coiled or very weakly developed and hardly visible. The glans penis is long and smooth (without spines). An os penis is present, straight and bears a groove on its upper surface.

The head is usually elongated with a long tapering muzzle. The ears usually have a sharp apex and are located fairly high, of moderate length, sometimes very long (longer than the head) and, as an exception, they may be short with rounded apex. The tail is of moderate length (to tarsal joint) or longer, rarely short, and is covered all along its length with long hairs (the hairs are shorter at the base). Cutaneous glands are weakly developed, the anal glands are few, sometimes absent, and there are no genital glands; in some species, there is a scent gland on the upper side of the tail ("violaceous" gland). A scrotum is present. There are 3-4-5 pairs of teats.

The pelage of northern forms, in winter fur, is long, dense, fluffy and frequently silky, whereas in the south it is usually more coarse and sparse. The general color is usually more or less monotone, gray, yellow and red tones, sometimes with a dark dorsal saddle; and as an exception, almost black or of large and bright irregular black, white and red spots. In some species there are several color phases.

There is no sexual dimorphism; age dimorphism in some species is rare in some or is quite sharply distinct. Seasonal dimorphism in forms of temperate and northern latitudes is considerable, manifested in the

¹According to some data, this species has 36-38-40 teeth (Haltenorth, 1958).

density and length of fur, and sometimes, in color (arctic fox). There are 1–2 molts per year.

In general constitution, species of the family are homogeneous, representing a variation of one type as a whole—the wolf type. The change in appearance is mainly determined by the proportion of the trunk length and that of legs, and in part, tail length.

The form with the most extremely long legs, resembling the borzoi dog, with a proportion of trunk length to shoulder height of about 1 : 1, is represented by the South American maned wolf (*Chrysocyon brachyurus*). The hunting dog of Africa (*Lycaon pictus*) is very close to it. The wolf is of the same type, but with shorter legs. The subsequent type is represented by our fox and related species, which are of still shorter legs and elongated trunk, with proportion equal to 1 : 0.5; they have a long tail. The last group is represented by species which are similar to the raccoon dog (*Nyctereutes procyonoides*), with the extreme in this form represented by the South American bush dog (*Speothos venaticus*). It has a somewhat “dachshund-like” appearance, with proportions of 1 : 0.3 or slightly more, and a short tail.

The species differ considerably in size. The largest species—wolf (*Canis lupus*)—has, in its large forms, body length to 160 cm, tail to 50 cm, height at the shoulders to 85 (100) cm and weight to 50–60 kg or sometimes, exceptionally, to 80 kg. The smallest form—fennec (*Fennecus zerda*)—has a body length of about 40 cm, tail of about 20 cm, height at the shoulders is about 20 cm and weight of about 2 kg. The proportions of extreme forms by weight is, in this way, about 1 : 25–30.

The wolf family in its full breadth of specialization, both as a whole and also in particular species, represents one of the relatively “generalized” groups of the order.

The majority of the species of the family are excellent runners, usually catching their live prey in open pursuit; some of them are very quick and have extremely great endurance in running. They are not adapted to climbing trees, and only the gray fox of America (*Urocyon*) can climb somewhat. Some dig quite well. They live in all landscapes, up to extreme high montane, but the majority, in all continents, are connected with the more or less open areas (forest steppe, steppe, desert). They frequently live individually, some live in pairs, and some species apart from the breeding season live and hunt in family groups or packs which are sometimes of great significance (hunting dog, *Lycaon pictus*; red wolf [dhole], *Cuon alpinus*).

The majority are sedentary, but some species accomplish considerable seasonal or irregular migrations or lead a nomadic life. They are monogamous animals, some species live in pairs for many years. The number of offspring [per litter] is up to 13–18 (according to some data up to 22–23), but is usually 4–7 and not more than 10. Males of the majority of species take part in the rearing of their offspring. This family is psychologically one of the most highly developed groups of carnivores, with definitely amicable internal relationships in packs and families, hierarchies, etc. This is, to a considerable degree, associated with the life in packs of many of the species.

They are principally nocturnal, frequently crepuscular and rarely diurnal. Vision is relatively weak, hearing very good, and the sense of smell is sharp to the highest degree. The fresh meat of small and middle-sized mammals constitutes their main food, but several feed on large ungulates, carrion and rarely insects and other invertebrates. They utilize plant food, mainly fruits and berries, as supplementary food.

The geographic distribution of the family is exceptionally vast—practically almost cosmopolitan. It corresponds to the geographic range of the order; however, the species of this family are absent from Madagascar, the entire Malayian archipelago with the exception of Sumatra and Java, the Philippines, Hainan, Taiwan and the Ryukyu islands. Occurrence in Australia (dingo) is secondary as a result of domestic dogs becoming feral (see characteristics of the order). In the north, the representatives of the family inhabit all lands and are found on oceanic ice nearly to the pole (arctic fox). On the Falkland Islands, they are extinct; several species (wolf) had their ranges reduced; however, the geographic area of the family as a whole did not essentially change since historical time.

The family represents an ecological quite plastic and quickly adapting flourishing group of carnivores. The decline in numbers as well as range reduction of some species occurs only as a result of excessive hunting and destruction. Besides, the wolf, for example, persists even in places with special hunts for its total destruction.

According to its systematic characteristics, the family occupies a quite distinct position and is sharply distinguished from other families. It is considered to be closest to the bear family, Ursidae. However, judging by some characteristics of the genus *Nyctereutes* (raccoon dog), the relation of this family to that of raccoons (Procyonidae) may be closer (Frechkop, 1959). The resemblance of some forms to the

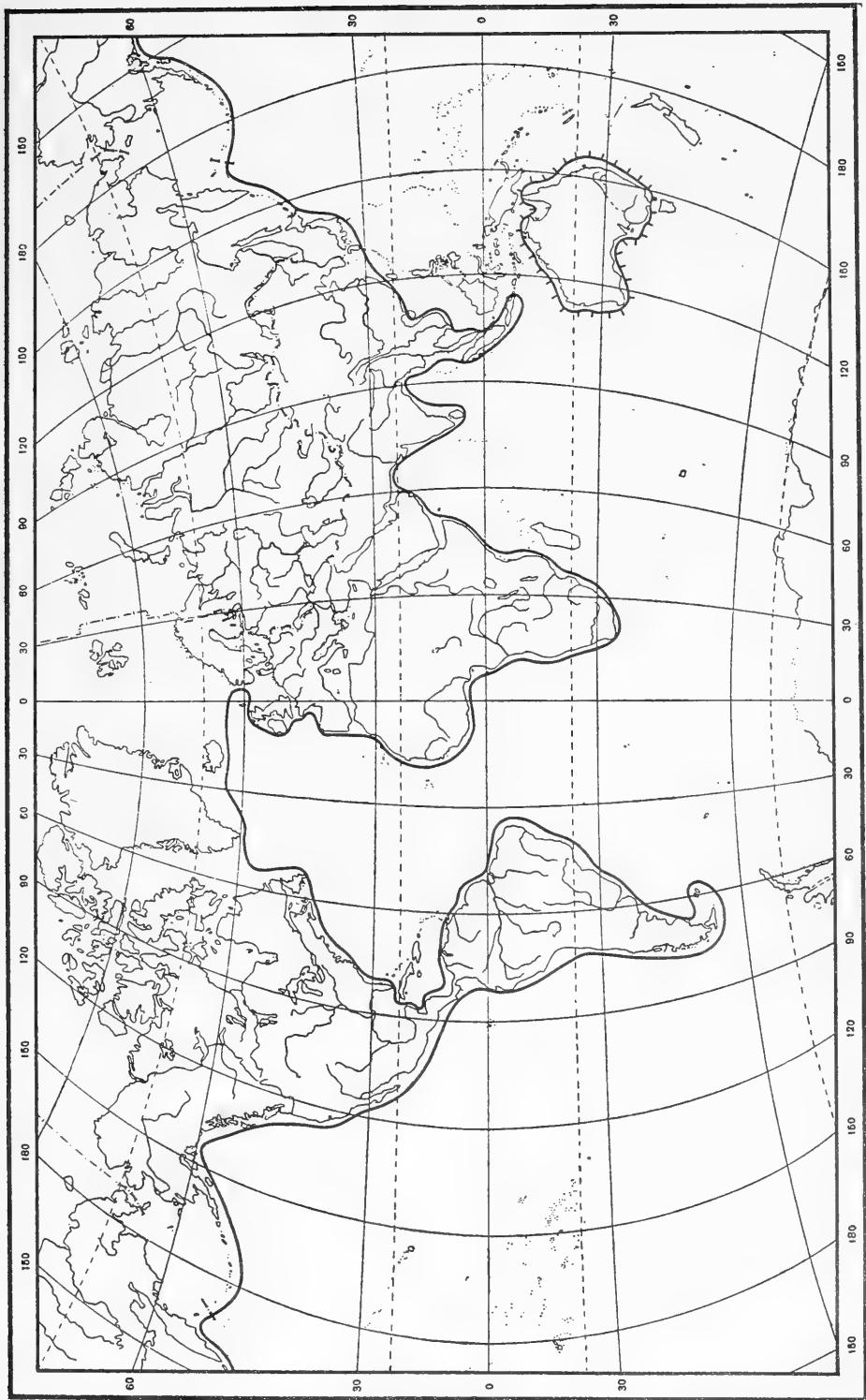
hyaena, Hyaenidae, is purely external, and is, to a certain extent, convergent.

Concerning their origin, Canidae is one of the most ancient branches of carnivores, already identifiable in the upper Eocene. The earliest forms (*Procynodictis*, *Cynodictis*) are very primitive and possess features indicating their relation to forms which lie in the root of all Carnivora = Fissipedia.

Concerning the internal systematic structure of the family, it is quite unified. Attempts were made to divide it into some families by separating such forms as the red wolf (*Cuon*) and hunting dog (*Lycaon*), bush dog (*Speothos*) and, mainly, the bat-eared fox (*Otocyon*); however, these attempts were poorly based and did not meet with acceptance.

62 The present division into subfamilies is fairly simple and is actually generally applicable. There are usually six subfamilies: the recent Caninae (wolves, foxes, raccoon dogs), Simocyoninae (Cuoninae, Lycaoninae—red wolves and others), Otocyoninae (bat-eared foxes) and three extinct ones: Amphicyoninae, Amphicyonodontinae and Borophaginae (Simpson, 1945). Sometimes, the genus *Speothos* (South American bush dog) which, in the above-mentioned system is related to Simocyoninae, is considered as a separate family—Speothoninae. Among the existing forms, this species is so peculiar that this point of view, supported most recently (Haltenorth, 1958), is represented as most justified.

However, this system—at least that concerning the recent forms—is not irreproachable. If the justified separation of the genus *Otocyon* with its extremely peculiar dental formula in a separate group is approved (see above), this cannot be applied in relation to Simocyoninae. The genus *Lycaon* (hunting dogs) of this group has the same dental formula as all other Caninae (42) but it has only four digits on the forelimbs (the metacarpal bone of the first digit is even reduced); genus *Cuon* (red wolf) has the same number of digits on the forelimbs as in Caninae, but the dental formula is somewhat reduced (40, see below). The differences in the skull structure of the members of these genera from that of all Caninae in general, are not more than the differences between the various forms of Caninae. The differences in the structure of MI (see below) are also not very considerable and have no principal significance. According to what has been previously mentioned, there is no sharp limitation between Simocyoninae and Caninae in the characteristics mentioned.



61 Fig. 13. Reconstructed geographic range of the family of wolves, Canidae. Line surrounding Australia denotes the range of the dingo ("*Canis dingo*").
V.G. Heptner.

The genus *Speothos* is better differentiated, first of all, by its dental formula (38, see above), which is still more reduced than that of *Cuon*, and by its “dachshund-like” appearance, blunt head, rounded ears, short tail, etc. This form is sharply different, not only from Caninae and Simocyoninae (*Cuon*, *Lycaon*), but also from the genera with which it is frequently included in one group. Combining the characteristics in the family allows us to think that it is more natural to divide this family into two subfamilies—Otocyoninae (*Otocyon*) and Caninae (all other Canidae)—or to three, but in a combination of form different from the adopted one: with the retention of *Cuon* and *Lycaon* in the Caninae, but with the separation of *Speothos* in a special subfamily—Speothoninae.²

The number of genera in the family estimated by various authors is different. Lately, 68 genera are accepted, of which 56 are extinct and 12 existing. Of the latter, eight genera belong to Caninae (*Nyctereutes*, *Canis*, *Alopex*, *Vulpes*, *Fennecus*, *Urocyon*, *Dusicyon*, *Chrysocyon*), three to Simocyoninae (*Cuon*, *Lycaon*, *Speothos*) and one to Otocyoninae (*Otocyon*) (Simpson, 1945). Some, mainly on account of the American forms, employ a greater number of genera. The actual number is, apparently, 7–8: Caninae—*Nyctereutes*, *Canis*, *Chrysocyon*; Simocyoninae—*Speothos*, *Lycaon*, *Cuon*; Otocyoninae—*Otocyon*. The other genera usually employed are only subgenera, mainly of the genus *Canis* (see below, Haltenorth, 1958).³ The total number of species in the family which was considered not long ago to be fairly large (about 45), equals 29; namely, 23 species of *Canis*, *Alopex* and *Vulpes*—without the dingo and, excepting further reallocations in generic characteristics—*simensis* (subgenus *Simenia*), *rueppelli*, *chama*, *pallida*, *zerda* (subgenus *Fennecus*), *microtis*, *thous* (subgenus *Lycalopex*), *cinereoargenteus*, *culpaeus*, *hagenbecki*, *australis* (*Dusicyon*), *Chrysocyon*—1 (*C. brachyurus*—South American maned wolf), *Nyctereutes*—1 (see below), *Speothos*—1 (*S. venaticus*—South American bush dog), *Lycaon*—1 (*L. pictus*—African hunting dog), *Cuon*—1 (red wolves; see below), *Otocyon*—1 (*O. megalotis*—African bat-eared fox).

²Systematic relationships in the family require special analysis, and here the traditional grouping of the species of our fauna into two subfamilies is conditionally given.

³The uniting of the genera *Cuon* and *Lycaon*, even without the application of subgeneric rank, suggested by the same author, is not accepted. It is possible that their union was based on the fact that the author wrongly applies the same dental formula for both genera (42), although in *Cuon* there are only 40 teeth.

Six species inhabit Asia (*V. cana*, *V. ferrilata*, *V. bengalensis**, *V. corsac*, *N. procyonoides*, *C. alpinus*); in Africa—seven (*C. simensis*, *V.** chama*, *V.** pallidus*, *C. adustus*, *C. mesomelas*, *L. pictus*, *O. megalotis*); in South America—seven (*D.*** microtis*, *D.*** thous*, *D. culpaeus*, *D. hagenbecki*, *D. australis*, *C. brachyurus*, *S. venaticus*); in North America—two (*V. velox*, *C. latrans*). One species lives in Eurasia, Africa and North America (*V. vulpes*), two species in Africa and Asia (*V.** rueppelli*, *F.** zerda*), two in Eurasia and North America (*C. lupus*, *A. lagopus*), one—in Africa and Eurasia (*C. aureus*) and one—in North and South America (*D. cinereoargenteus*).

Among the species of the family there are exploited animals which give fur, usually expensive, and—to a lesser degree—are objects for sport hunting. Some species are important destroyers of rodents. A considerable number of them have no noticeable utility and, in general, any practical significance. Some species are dangerous pests for livestock breeding and the hunting economy, and some are reservoirs for rabies virus, transmitting it to domestic animals and man.

One of the species (wolf) has its geographic range considerably decreased in connection with its eradication in many places both in the Old and New World, and another one, Falkland wolf, *Canis (Dusicyon) australis*, is completely extinct. The geographic range of some species has increased in connection with their acclimatization (red fox). One species is present in a wild form as well as in a completely domestic form (wolf-dog) and two species are present in a wild and semi-domestic form as objects of fur-farming (red fox and polar fox).

In the USSR fauna, 2 of the 3 subfamilies are represented: Caninae and Simocyoninae; 5 of the 12 existing genera (42%)⁴: *Nyctereutes*, *Canis*, *Alopex*, *Vulpes*, *Cuon*, and 8 species of 29 (about 27% of the species of the family); they constitute about 2.6% of the total number of species of our fauna.

The geographic range of this family covers the whole territory of the USSR and its species are found under all natural conditions, to extreme high montane regions and the ice of the Arctic Ocean.

*Misspelled *lengalensis* in Russian original—Sci. Ed.

**Spelled *F.* probably for subgenus *Fennecus*, in Russian original—Sci. Ed.

***Spelled *L.*, probably for subgenus *Lycalopex*, in Russian original—Sci. Ed.

The treatment of genera and subgenera is inconsistent—Sci. Ed.

⁴Or 3 out of 7, i.e., 43%

The species of the family have an important value in the USSR as fur-bearing and sport hunting animals, destroyers of rodents, pests for animal breeding and hunting and carriers of some diseases (V.H.).

Key for Species Identification of the Wolf Family

- 1 (2). Six teeth (premolars and molars) behind canine on lower jaw; total number of teeth 40. Condylbasal length of skull not less than 170 mm. General dimensions slightly less than those of wolf. Color bright reddish-yellow; dorsal side of ear of same color. On fore limbs, pads of middle digits connected posteriorly by an anastomosis (Fig. 17)red wolf [dhole], *Cuon alpinus* (p. 571).
- 2 (1). Seven teeth behind canine in lower jaw; total number of teeth 42.⁵ Color different; if red, dorsal side of ear black.
- 3 (4). Posterior lower angle of lower jaw below angular process with sharp, deep angular groove (Fig. 14). Muzzle with dark, mask-like shading, also covering eye region. Size similar to foxraccoon dog, *Nyctereutes procyonoides* (p. 82).
- 64 4 (5). No sharp angular groove on posterior lower angle of lower jaw, or only a very gently sloping, not deep arciform groove. Dark "mask" on muzzle covering eye region absent.
- 5 (8). Frontal (interorbital) region of skull noticeably elevated relative to nasal region, and line of upper profile of skull forms protrusion here. Postorbital processes convex above. Apex of lower canine, when jaws are closed, does not reach margin of alveolus of upper canine. Facial part of skull relatively short and broad (distance from posterior margin of preorbital foramen to posterior margin of canine alveolus less than width of skull above canines).
 Tail with hair equal to or shorter than half of body length. On undersurface of hind foot, five large bare pads (callosities), four digital and one behind them. Pupil rounded.
- 6 (7). Arcuate line formed by anterior margins of nasal bones lacks sloping middle process (near suture of both bones). Protruding cingulum on outer side of base of first upper molar (second tooth from rear) narrow and blunt with median constriction or

⁵As an individual difference, the number of molars and premolars may be 6. However, in this case, the longest skull is 125 mm.

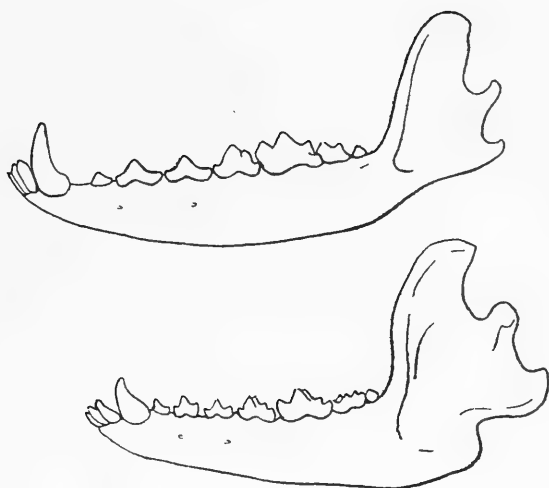


Fig. 14. Lower jaw of fox, *Vulpes vulpes* L., and raccoon dog, *Nyctereutes procyonoides* Gray, below (schematic). The deep notch on the lower posterior angle of the jaw of raccoon dogs is shown. Sketch by N.N. Kondakov.

gap. On fore limbs, pads of two middle digits not united by commissure in posterior part (Figs. 15, 16, 17).

Dimensions large, skull length more than 200 mm; total body length of adults more than 90 cm. Tail length almost half of body length wolf, *Canis lupus* (p. 164).

- 7 (6). Arcuate line formed by anterior margins of nasal bones has in middle (at suture of bones) small blunt and anterior projection. Cingulum on base of first upper molar wide, sharply defined and without gaps. On fore limbs, pads of two middle digits are connected by commissure in posterior part (Figs. 15, 16, 17).

Dimensions smaller, skull length not more than 190 mm; total body length of adults less than 90 cm.⁶ Tail length is about half that of body jackal, *Canis aureus* (p. 129).

- 65 8 (5). Frontal (interorbital) region of skull not noticeably elevated relative to nasal region, and line of upper profile of skull relatively uniformly elevated towards rear. Postorbital processes flat or concave above. Apex of lower canine, when

⁶In the species, as a rare exception, body length may be somewhat larger. In such case, identification is decided on skull size, structural craniological characters, and structure of the pads of the fore limbs.



64 Fig. 15. Anterior margin of nasal bones of wolf (to the left) and jackal—dorsal view. Sketch by N.N. Kondakov.



65 Fig. 16. Cingulum of anterior upper molar of wolf (above) and jackal. Sketch by N.N. Kondakov.



65 Fig. 17. Sole and digital pads of fore limb of wolf, jackal and red wolf (left to right). Sketch by N.N. Kondakov.

jaws are closed, reaches margin of alveolus of upper canine or extends beyond. Facial part of skull relatively narrow and long (distance from posterior margin of preorbital foramen to posterior margin of canine alveolus more than or equal to width of skull above canines).

Tail with hair exceeds half of body length. Undersurface of hind foot has only 4 circular, bare digital pads (callosities). Pupil oval, vertical.

- 9 (10). Postorbital processes above flat or slightly concave. Apex of lower canine, when jaws are closed, reaches only margin of alveolus of upper canine or extends a bit farther above it (Fig. 18). Distance from posterior margin of infraorbital foramen to posterior margin of canine alveolus equal or almost equal to skull width above canines.

Ear with rounded tip, relatively short; when bent forward, tip does not reach eye. Body color either completely white or evenly brownish-gray (winter fur), or back, limbs and tail are brownish while side and venter are dirty whitearctic fox, *Alopex lagopus* (p. 274).

- 10 (9). Postorbital processes above strongly concave (at base, dorsal groove is formed). Apex of lower canine, when jaws are closed, extends considerably past margin of upper canine alveolus. Distance from posterior margin of infraorbital foramen to posterior margin of canine alveolus greater than width of skull above canines.

Ear with sharp tip, long; when bent forward, tip reaches eye. Color different.

- 11 (12). Posterior side of ear brownish-black or pure black and sharply distinguished from red or sandy-reddish color of back. Black markings on anterior side of fore limbs. Extreme tip of tail, at least very small part, white. Size relatively large; body length more than 65 cm, total length of skull more than 115 cm, width of zygomatic arches more than 64 mm.red fox, *Vulpes vulpes* (p. 469).

- 12 (11). Posterior side of ear not black or brownish-black and not distinguished from color of back. No black marks on anterior side of fore limbs. Tail tip not white. Size smaller.

- 13 (14). Back gray mixed with black (in form of ripples). Chin and lower lip dark brown or black. Canines very long; when jaws are closed, ends of upper canines protrude beyond level of

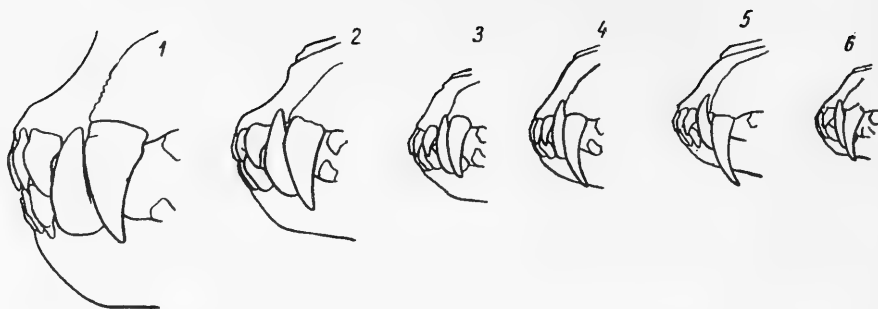


Fig. 18. Canines and incisors from side* (Sketch by N.N. Kondakov). 1—wolf; 2—jackal; 3—arctic fox; 4—Middle Russian red fox (*Vulpes vulpes vulpes* L.); 5—Turkmenian red fox (*V. v. flavescens* Gray); 6—Corsac fox.

- lower margin of lower jaw. Size very small; body length less than 50 cm, skull length less than 95 mm, zygomatic width less than 50 mm Afghan fox, *Vulpes cana* (p. 390).
- 14 (13). Color of back is rusty or rusty-yellowish, grizzled from the white ends of the guard hair. No mixture of black color. Chin and lower lip white. Canines relatively shorter. Ends of upper canines, when jaws are closed, reach level of lower margin of lower jaw. Size larger; body length more than 50 cm, skull length more than 95 mm, zygomatic width more than 58 mm corsac fox, *Vulpes corsac* (p. 396) (V.H.).

Subfamily of Wolves

Subfamilia Caninae Gill, 1872

Genus of Raccoon Dogs, or Manguts

Genus *Nyctereutes* Temminck, 1839

1839. *Nyctereutes* Temminck. In: Van der Hoeven's Tijdschr. Nat. Ges. Phys., 5, p. 285. *Nyctereutes viverrinus* Temminck.

Forms of small size.

Skull relatively quite heavy and massive, moderately elongated, with narrow zygomatic** arches, and not high (height in occipital

*In Russian original, "front", an apparent *lapsus*—Sci. Ed.

**"auditory" in Russian original, an obvious *lapsus*—Sci. Ed.

region little more than one third of condylobasal length). Protuberances and crests of skull well developed, sagittal crest high in old animals and occipital quite considerable.

Facial region of skull short and its length nearly equal to cranial—
 67 distance between anterior end of premaxillae and line connecting ends of supraorbital processes equal or nearly equal to that between this line and upper margin of foramen magnum. Facial region of skull massive. Distance between posterior wall of infraorbital foramen and posterior margin of canine alveolus less than width of skull above canines or equal to it.

Interorbital (frontal) region elevated, somewhat swollen in region of frontal sinuses between supraorbital processes; processes themselves not large, flat or slightly concave above, with tip sharply recurved downwards. Upper profile of skull at first almost straight and then becomes convex arcuate line; at anterior of nasal region already abruptly elevated and no frontal shelves occur. Posterior edge of tooth row does not reach level of anterior border of interpterygoid notch. Hard palate extends backwards behind line uniting posterior points of last molars to approximately 1/3 the distance between inner corners of last molars.

At lower edge of lower jaw, anterior to angular process, a large, massive protuberance, separated from angular process by deep angular notch. Such a mandibular structure also present only in American gray fox, *Dusicyon (Urocyon) cinereoargenteus** (Fig. 14). Angular process large and massive, with broad base and without upwardly directed denticle.

Dental formula: $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42$. As a fairly rare individual

deviation, there may occur $M \frac{3}{3} = 44$. Teeth relatively small and weak.

Upper canines strong, but short, their ends far short of upper border of lower jaw, and slightly curved; their ends not directed straight downwards, but somewhat slanted to the side. Cutting edge on posterior side of canine and on lateral surfaces, a blunt, smooth vertical edge. Upper carnassial teeth relatively weak. Incisors have no additional blades; external [third] incisor not adjacent to second, and separated from it by noticeable gap.

*Mispelled *cinereoargentatus* in Russian original—Sci. Ed.

Trunk long, legs short, and tail hangs below tarsal joint, but when the animal is standing, does not reach ground. Ears of moderate length.

Pelage (in northern forms) dense and fluffy in winter. Molt occurs once a year. Five pairs of teats. Intestine relatively long, compared to body length being 4.3 : 1 (Korneev, 1954).

Inhabitants of closed landscapes—forests, river valleys, preferably moist. Of low mobility, and travel relatively slowly. They do not perform regular migrations. Monogamous animals, pairing for one breeding season. 10–15 offspring, usually less. Young born in burrows, and they are associated with the burrows throughout the entire year. Apart from the period of reproduction, they live singly. They are predators, feeding on small vertebrates, especially rodents, amphibia, eggs, insects and other invertebrates, and also on berries and fruits. In the northern part of their range, they hibernate (the only species in the family).

The natural range of this genus is not great and is limited to part of eastern Asia. It occupies the southern parts of the Amur [and] Ussuri territories, northeastern China (former Manchuria), the Korean peninsula, eastern China to the extreme south, and the Japanese islands.

In the last ten years, the range has significantly expanded due to acclimatization in almost the whole European part of the [Soviet] Union and in the Caucasus, in separate places in southern Siberia and the eastern part of Middle Asia (see below; description of species).

Because of its systematic characteristics the genus *Nyctereutes* represents a strongly deviant form of the subfamily and stands completely apart. In any case the genus is more isolated from other genera of the subfamily than they are from each other. Even by broad interpretation of the genus, when such groups as *Vulpes*, *Alopex*, *Fennecus*, *Simenia*, *Lycalopex* and *Dusicyon* are included in the genus *Canis* (see characteristics of the family), the generic independence of *Nyctereutes* remains obvious and undoubted.

The genus may be considered specialized in some respects; however the more basic features, mainly in the structure of the facial part of the skull, in dentition, and in some other characters, are primitive. The genus ought to be included among the least specialized in the subfamily (family ?) and at the base of the systematic series. Also primitive are such characteristics as poorly developed predatoriness, low mobility (the animal is essentially not a predator, but a “collector”), large number of young and hibernation. Apparently, it is sufficiently basic to consider the genus as archaic and relict. This is supported by its geographic range, which is associated with a region in which Tertiary relict forms are preserved.

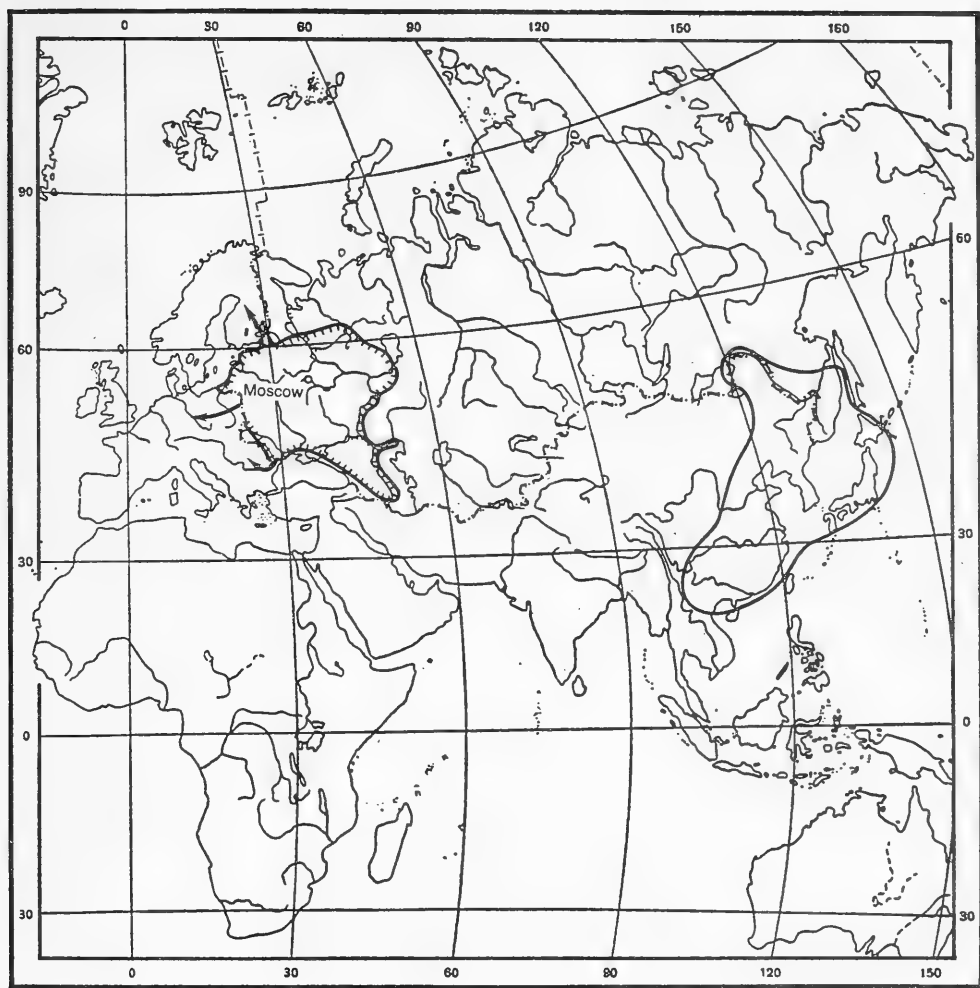


Fig. 19. Geographic range of the mangut, or raccoon dog, *Nyctereutes* Temm. In the east, the natural species distribution of the mangut; in the west, the region inhabited by acclimatized animals in the European part of the Soviet Union and in the Caucasus. Arrows point to the direction of spread of the raccoon dog from the USSR to Finland, Poland, Romania and Central Europe. (V.G. Heptner).

69 *Nyctereutes* has some characters similar to those of the raccoon family, Procyonidae. Thus, both in general outlines and some structural details, the skull of *Nyctereutes* resembles that of *Bassariscus* (cacomistles), and the dentition occupies, in a certain sense, an intermediate position between that of the true Canidae (*Vulpes*) and Procyonidae (*Procyon*). The biological characters noted, especially

hibernation, are also "raccoon" features (Frechko, 1959). These characters do not provide a basis for including *Nyctereutes* in the raccoon family, but they well emphasize the individuality of the genus. Moreover, they show that the relationship between the two named families is closer than what is usually believed.

Fossil representatives of the genus are not known. However, it can be assumed that the time of their development is concerned with the Pliocene, and perhaps even earlier.

The genus included one species: *Nyctereutes procyonoides* (Gray, 1834),* i.e. about 3.4% of the species of the family. This species constitutes about 0.3% of the species of the USSR fauna.

The natural range of the genus in the USSR is restricted to a small strip of forests of the Manchurian type in the Ussuri and Amur territories. This species has been acclimatized in other parts of the USSR (see below).

It is one of the secondary fur-bearing animals; useful to a certain degree in destroying rodents, but it is essentially harmful to the wild game economy (V.H.).

USSURI RACCOON, RACCOON DOG, MANGUT⁷

Nyctereutes procyonoides Gray, 1843

1843. *Canis procyonoides* Gray. Illustr. Zool., 2, pl. 1. Vic. Canton.
 1907. *Nyctereutes ussuriensis*. Matschie, Wiss. Ergebn. Forsch. nach China, 10, p. 178, Near Ussuri mouth.
 1907. *Nyctereutes amurensis*. Matschie. Ibid., p. 179. Amur.
 1958. *Nyctereutes procyonoides kalininensis*. Sorokin. Byull. Mosk. obshch. ispyt. prirody. Kalinin Department. 1. Kalinin district. (V.H.).

Diagnosis

Only species of the genus.

*In Russian original "Temmink, 1839"—Sci. Ed.

⁷First and second names are artificial and literal. "Raccoon dog" is simply a translation from the Latin—*Canis procyonoides*. It is the most common name in our literature. "Ussurian raccoon" is a furrier's term. The Russian local (Amur Cossack) name is "enot" [raccoon] (Cherkasov, 1867). Mangut is an Evenk name. It is better than the others, and was used by Russians. Unfortunately, it is not used in literature at the present time.

Description

General appearance of the Ussuri raccoon is entirely unique, not resembling the appearance of other representatives of the family. The trunk is long, legs short and they look particularly short in the animals with winter fur, which on the trunk is very long. Accordingly, the body has a massive appearance. Also, the legs are covered with short hairs and they look very thin. This gives the impression of a stocky and clumsy animal on short, thin legs.

70 The fur in winter is not proportional to the size of the animal. It is long (length of guard hair to 120 mm), thick, with dense underfur and coarse guard hair, shaggy and stiff. The tail is relatively short—not more than 1/3 the body length, its end falls below the tarsal joint, but it does not reach the ground when the animal is standing. The hairs of the tail are very long and dense, not shorter at the base than on any other part of its whole length and the tail fur is not clearly distinct from, and is transitional to, the fur of the croup. This reinforces the impression of a general elongation of the animal's body. The head is not large, with short, but pointed muzzle covered with short hairs. Behind the eyes the hair rapidly increases in length and quantity, and quite large ears, blunted on the ends, protrude slightly from the fur. There are large



Fig. 20. Mangut, or raccoon dog, *Nyctereutes procyonoides* Gray. Sketch by A.N. Komarov.



Fig. 21. Male mangut, 10–11 months of age. “Kedrovaya Pad’ ” preserve (southern Primor’e). March 1964. Photograph by A.G. Pankrat’ev.

“side-whiskers” of elongated hairs on the cheeks. The pointed muzzle looks as if it is emerging from the long fur of the head.

The general color tone of the winter fur is dirty, earth-brown or brownish-gray with a more or less considerable overlay of black (color of guard hairs). The tail is considerably darker than the trunk. Along the back extends a darker stripe which broadens on the shoulders, forming there an unclear cross-shaped figure. The abdominal surface is yellowish-brown and the chest is dark brown or blackish. Ears are black posteriorly. In the eye region, in front of them and on the cheeks below and behind the eyes and crossing the “side-whiskers”, is located a dark (almost black) field. Together, they form on the muzzle of the mangut a characteristic picture in the form of a mask which contrasts sharply with the brighter color of the muzzle and remaining parts of the head. This picture in particular, and the general color tone gives the described species a certain similarity to the American raccoon.

- 72 In summer, during the transition from one winter coat to another, the mangut has at first (first half of summer) only a pelage of dry lifeless top hairs (underfur sheds first) and later, the fur is formed of short, incompletely grown guard hairs, almost without underfur. Such hairs are several times shorter than winter ones. The color during that

time resembles that in winter, but its general tone is brighter, reddish-straw, but with a mixture of blackish-brown. The dark color forms a stripe along the back and dorsal side of neck, and a cross-shaped figure in the shoulder region. The chest is brownish-black while the belly and groin are brownish-gray with yellowish. The legs are blackish-brown, the "mask" is well defined; the chin, neck and chest are black. On the sides of the neck the color is quite bright, pale-rusty. Claws are light-horn.

For description of skull, see description of the genus. The diploid number of chromosomes is 42.*

Relatively speaking, data on the dimensions and weight of manguts are extremely scanty. Body length is about 65–80 cm; tail length, 15–25 cm; weight in summer 4–6 kg and in winter, 6–10 kg (C. Naumov and Lavrov, 1948).

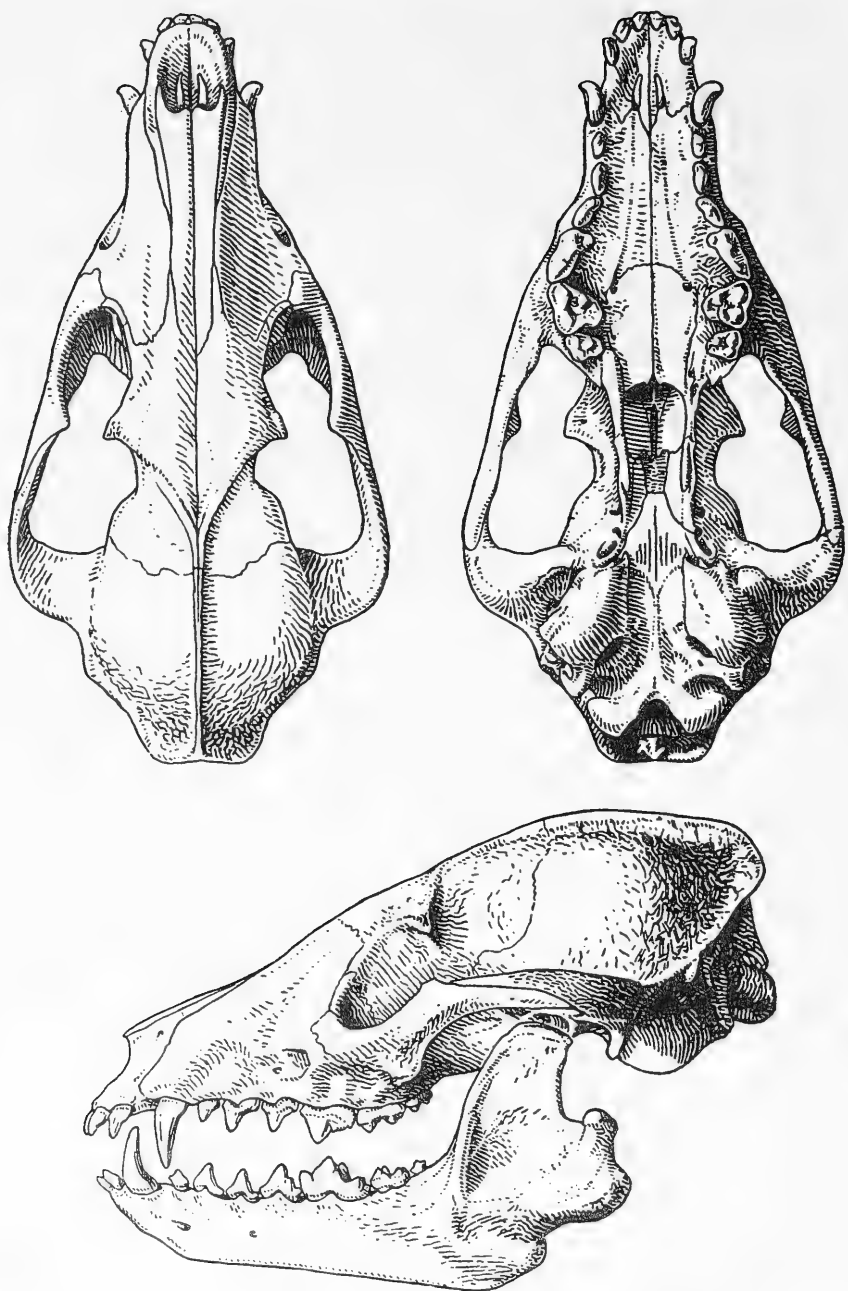
Dimensions of the skull (in mm) of males from the Far East are as follows (42 specimens; Sorokin, 1958):

	Range	Mean
Greatest length	114.3–131.8	123.4 \pm 0.6
Condylbasal length	103.2–125.8	119.2 \pm 0.6
Zygomatic width	61.0– 75.0	67.2 \pm 0.4
Width of muzzle between canines	20.3– 24.9	22.3 \pm 0.1
Width between orbits	19.8– 25.2	22.6 \pm 0.1
Distance between supraorbital processes	26.0– 36.0	31.5 \pm 0.3
Greatest width of skull	40.4– 44.5	42.3 \pm 0.1
Length of nasal bones	35.4– 50.7	42.6 \pm 0.4
Height of skull in region of auditory bullae	41.3– 48.3	44.6 \pm 0.2
Length of upper tooth row	42.7– 49.4	46.4 \pm 0.2

Dimensions of the skull of females from the Far East
(40 specimens):

	Range	Mean
Greatest length	112.8–131.7	120.3 \pm 0.6
Condylbasal length (36)	110.1–126.6	109.8 \pm 0.5

*Now known to be 38 + 1–4 small B chromosomes for Japanese animals. Mainland raccon dogs have a diploid number of 54 + 1–3B chromosomes—Sci. Ed.



71 Fig. 22. Skull of mangut, or raccoon dog, *Nyctereutes procyonoides* Gray.

	Range	Mean
Zygomatic width	60.2— 71.3	66.2 \pm 0.4
Width of muzzle between canines	18.7— 23.8	21.5 \pm 0.1
Width between orbits	19.5— 25.5	22.3 \pm 0.2
Greatest width of skull	38.9— 45.3	42.1 \pm 0.2
Length of nasal bones (39)	37.2— 49.7	43.6 \pm 0.4
Height of skull in region of auditory bullae (39)	41.0— 47.6	44.6 \pm 0.2
Length of upper tooth row	43.2— 51.7	45.8 \pm 0.2

Difference in the dimensions of males and females is so small that sexual dimorphism is basically not evident (V.H.).

Systematic Position

See characteristics of the genus.

Geographic Distribution

The forest areas of eastern Asia from the Amur territory to northern Indochina. This is a typical range for a species of the Manchurian-Chinese fauna.

As a result of acclimatization, a new range was established in the European part of the [Soviet] Union and in the Caucasus, and there are separate sections of occurrence in Siberia and Middle Asia.

Geographic Range in the Soviet Union

The range in the USSR represents the extreme northern border of the range of the species. It is not large, and occupies a very small part of the country; namely the Ussuri territory and the southern part of the Amur.

73 The outlines of the range within the territory of the [Soviet] Union are fairly complicated. In the east it begins at the Pacific coast of the Ussuri territory in the region of the mouth of the Tumnin river (about 51° N. Lat.) and extends as a narrow strip along the seacoast to the south and southeast along the foothills and lower mountain belt. Passing around the higher parts of the southern extremity of Sikhote-Alin' from the south and approximately in the latitude of the northern end of Lake Khanka, the boundary traverses the western slope of the range. Along the Ussuri valley and along the western slopes of Sikhote-Alin',

the range strip passes north to the Amur and reaches it at the mouth of the Ussuri. Along the valleys of the more significant right tributaries of the Ussuri (Bikin, Khor, Iman), the range at places extends far to the east into the mountains; however, the mangut is absent in the extreme high-montane Sikhote-Alin', and in the region of the extensive coniferous forests.

Along the Amur valley and adjacent places, the range extends northward (downstream) nearly to the Khungara. From this place the northern border of the range continues westward through the Burein mountains and the middle course of the Bureya and Zeya to the Amur in the region of the junction of the Shilka with the Argun. Because of scanty information, it is impossible to determine whether the species described is distributed all along the Amur valley to the west from the Zeya, or whether they penetrate from the south (from China) to the mouths of the Shilka and Argun. They are not found in the extreme northern part of the northern bend of Amur. According to some data, the northern border of the normal occurrence extends in our country from the east only to the mouth of the Khumaerkhe on the Amur. To the south, the range extends everywhere up to the state boundary.

The mangut is absent in Trans-Baikal, although in remote times, it apparently reached the upper Onan.⁸ Sakhalin is not included in the natural range.

In the last decades (starting from 1934), the Ussuri raccoon increasingly has been established, especially in the European part of the [Soviet] Union, and also transplanted to separate places in the Asiatic part. At the present time in the European part of the country, the mangut formed a vast distribution area, which considerably exceeds its natural range within the USSR.

In the north the new range occupies all of Karelia and, probably, the entire southern part of the Kola peninsula, the whole of Arkhangel'sk district including the forest-tundra; however, incursions by the mangut onto the tundra occur. Apparently, the northern border passes somewhat more to the south along the Pechora. In the west, the range in the entire European part of the Union reaches the western state boundary and in some places beyond it. In the south, the range reaches the Black, Azov and Caspian seas. The eastern border is less defined. On the

⁸Old data about the permanent habitation of the animal here were not confirmed. The range is according to Cherkasov, 1867; Radde, 1862; Maak, 1859; Schrenk, 1858; Ognev, 1931; C. Naumov and Lavrov, 1941; material of N.N. Rukovskii and other sources.

northeast, the mangut is known (settled) at the river Ishma (left tributary of the Pechora). To the south, the border extends, apparently, along the Urals west of the range—through Perm district and Bashkiriya to Orenburg. From the Urals it extends to the Volga and follows it down to the [Caspian] Sea. The line of the eastern border of the European range is very undefined, not only due to insufficient information, but also because it changes as a result of introductions of the animal (easternmost transplantations: Syktyvkar, Udmurtiya, Ufa, Orenburg).

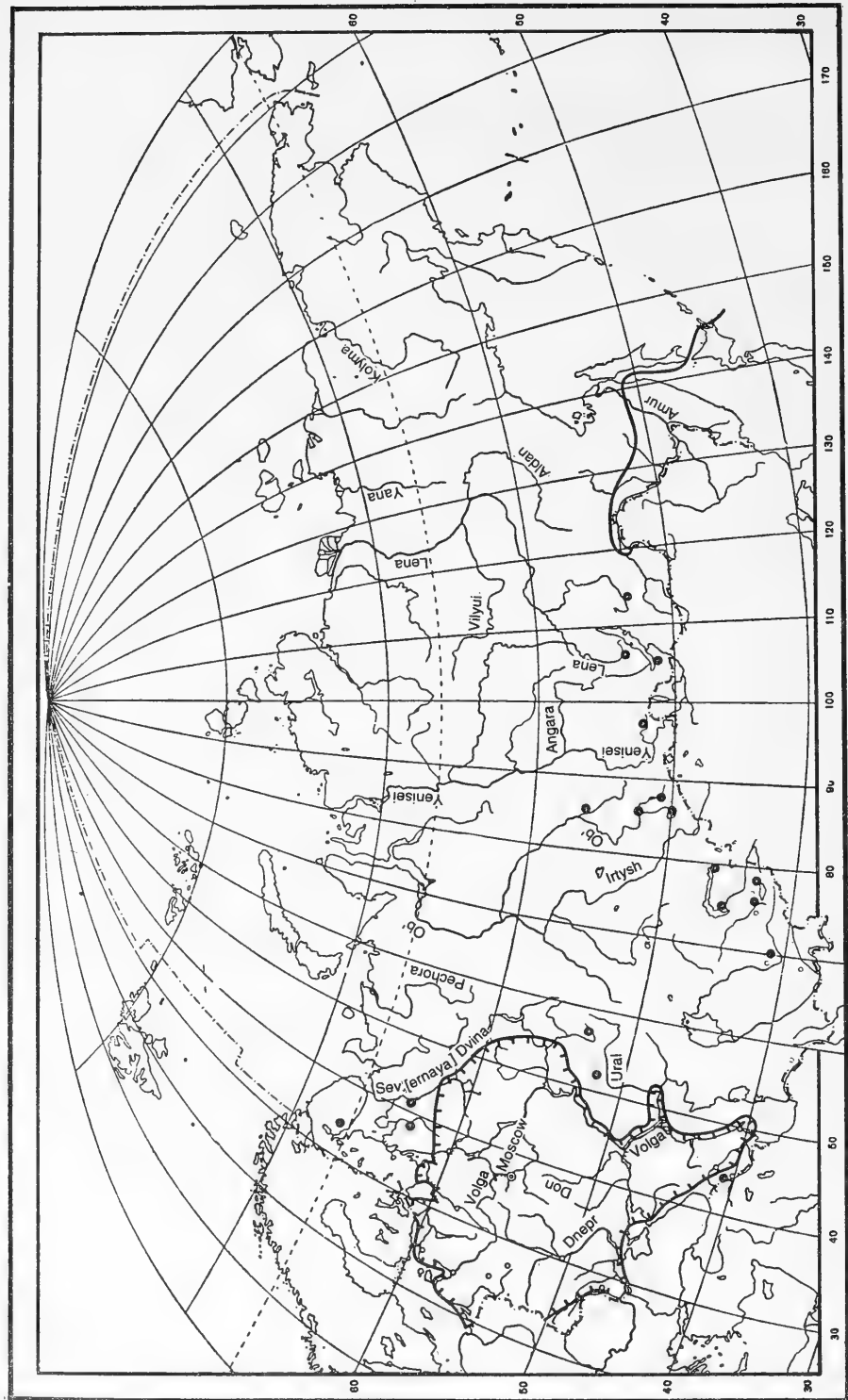
Within the outlined borders, by 1960 mangut actually occurred everywhere. If it was still absent in more or less considerable parts (some parts of Karelia and Cis-Urals) or its distribution was sporadic or it was very rare (Arkhangel'sk district), then in most of the area (several districts) its number increased immensely and it became an important enemy of the hunting economy.

In the Caucasus, the Ussuri raccoon has been transplanted and established in a series of places. Its range extends into the Cis-Caucasian steppes and foothill districts, and the eastern half of Trans-Caucasus. It is, apparently, absent only in the western part of Georgia. Its occurrence within these outlined boundaries is not continuous.

- 75 Outside the above-described borders, Ussuri raccoons were established in Middle Asia and Kazakhstan—to the east of Frunze, in Issyk-Kul, in the Dzhelalabad region, at the mouths of the Ili and Lepsa, to the south of Alma-Ata, in the Dzhungarsk Alatau, and in Katon-Karaga region in the southwest Altai.

In Siberia, manguts have been established at the mouths of the Biya and Katun, and in a series of places in the Altai, near Tom'sk at the sources of the Tom', near Novosibirsk, near Krasnoyarsk, in Tuva, at Irkutsk, northeast of Ulan-Uda and along the Dzhida and even in Yakutiya—at the mouth of the Vilyui and southeast of Suntar on the Vilyui. They were also acclimatized in several other places, including Sakhalin.⁹ Establishment in Siberia and Middle Asia did not lead to the formation of significant patches of occurrence, to say nothing of a continuous range. In the majority of places, apparently, the animals died or are dying, and in some places, small foci were formed.

⁹Acclimatization of the mangut from data of Lavrov, 1946; Rukovskii, 1950; Korneev, 1954; Vereshchagin, 1959; Berens and Yakushevich, 1959; Marvin, 1959; and a number of other works as well as the materials provided by N.N. Rukovskii.



Geographic Range outside the Soviet Union

The range outside the USSR includes China, from former Manchuria southward to Fukien, Guandong and Yunnan, the Korean peninsula, the northeastern part of the Indochina peninsula (Tonkin, now Bakbo province in North Vietnam). Borders of the distribution to the west are undefined; in northeast China the range does not go beyond Great Khingan (absent in the Mongolian Republic); to the south, it is known from Shaanxi and Sichuan; absent in Burma. It is found in the Japanese islands (Honshu, Shikoku, Kyushu, but is absent on the Ryukyus). It is not present on Taiwan and Hainan.

As a result of the spread of the animals acclimatized in the European part of our country, at the end of the 1950's the Ussuri raccoon penetrated to Poland, Romania, Finland, northeast Sweden and even in the G[erman] D[emocratic] R[epublic], where they are found east of Berlin (V.H.).

Geographic Variation

Geographic variation of the species is not well studied. Five subspecies are usually accepted. Within the Soviet Union one subspecies is present.

Ussuri mangut, *N. p. ussuriensis* Matschie, 1907 (syn. *amurensis*, *kalininensis*).

For description, see above.

Ussuri and Amur territories. Acclimatized in the European part of the USSR and in the Caucasus.

Outside the USSR, northeast China and Korean peninsula; the limits of distribution to the south are unclear.

This form is poorly described, but by comparison with the nominal form from the extreme south of the range it apparently is distinguished by the somewhat larger size and denser, longer hair. There is no comparative study of our form. The name *amurensis* is based on an occurrence character.

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- 74 Fig. 23. Range of the mangut, *Nyctereutes procyonoides* Gray in USSR. Continuous line in the Far East is the northern border of the natural range of the species. The more or less continuous distribution formed as a result of acclimatization in the European part of the country and in the Caucasus is shown by the closed line in the West. Individual dots are the places of establishment of the animals beyond the limits of the western range. Data of the western part of the distribution area are from the beginning of the 60's. (V.G. Heptner).

Separation of animals from Kalinin district in the form of an independent subspecies *N. p. kalininensis* (Sorokin, 1959) was unnecessary and uncalled for. As is evident from the figures given by the author, there is no difference in the dimensions of the skull. Differences in the quality of fur (longer, fluffier, softer and denser) are very difficult to perceive. If differences exist, they mainly reveal completely normal phenotypic variability. The independence of this form has neither a practical nor theoretical basis.

Outside the boundaries of the USSR, the following forms are usually accepted: (1) *N. p. procyonoides* Gray, 1834—China, except Yunnan, Tonkin; (2) *N. p. viverrinus* Temm., 1844—Japanese islands; (3) *N. p. koreensis* Mori, 1922—Korean peninsula; (4) *N. p. orestes* Thos., 1923—Yunnan. The reality of the last two forms, especially the Korean one, is highly doubtful. Most probably there are 3 forms—the mainland southern (*procyonoides*), northern (*ussuriensis*) and island (*viverrinus*). (V.H.).

Biology

Population. There are hardly any data about the number of raccoon dogs within the limits of its natural range in the Far East. The densest population is observed in the southwestern part of Primorsk territory, south of Lake Khanka, in the lower and middle courses of the Iman, Bikin, and Khor rivers and the middle course of the Amur River. In the basins of the Maikhe and Suchan rivers and along the coast of the Japanese Sea south of Nakhodka Bay (Ussuri territory) in 1931, the population density (calculated by the number of burrows found) consisted in various habitats of from 0.9 to 8 animals, averaging 3.4 per 1000 hectares. On Askol'd Island, density averaged 3.8 animals over the same area [i.e., 1000 h] (Bannikov, 1964).

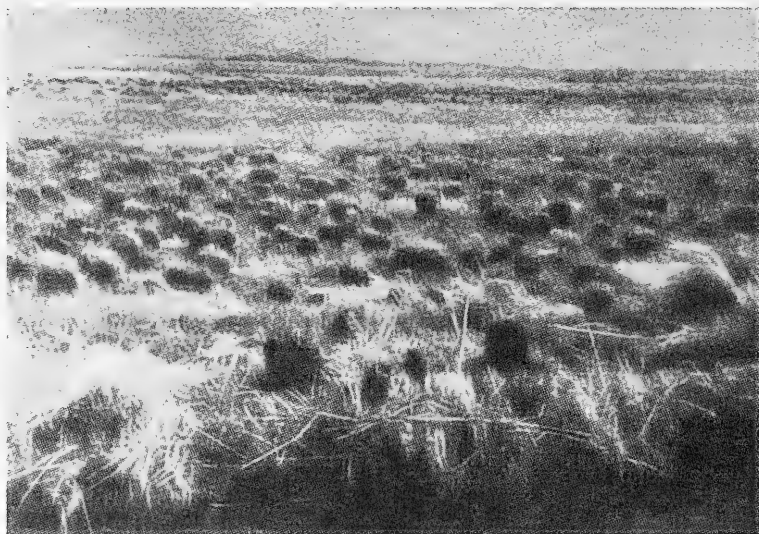
In the majority of regions of acclimatization of this species in the European part of the USSR, in the zone of mixed and deciduous forests, the population density constitutes about 1–2 animals per 1000 hectares. In the flooded deciduous forests of some regions, for example Novgorod (Morozov, 1953), it reaches 13 individuals per 1000 hectares; in the middle Volga region and Tatariya, 2–3 animals (V. Popov, 1953), in Gor'kovsk district, in different years, from 15 to 48 (Kozlov, 1952); in Voronezh district an average of 1–2 animals per 1000 hectares, but in some regions, for example Bogucharsk, to 20 individuals in such an area (Obtemperanskii, 1953; Ivanova, 1962). In the northeastern

regions of Lithuania, 5 to 10 animals were counted in 1000 hectares of forest area; in the northern regions, 2–4 individuals; and in the southern and western regions, about 0.5 per 1000 hectares (Prusaite, 1961).

In Rostovsk district and in the Ukraine, the population density of raccoon dogs consists of 2–5 animals per 1000 hectares of land. However, on the forested islands and along the shores of water bodies, it reaches 29–46 animals (Rall' and Kritskaya, 1953; Korneev, 1954; Sergeenko, 1956 and others). In the northern Caucasus, in Dagestan, Georgia and Armenia, Azerbaijan and Moldavia, the number of raccoon dogs, as a rule, does not exceed 1–2 individuals per 1000 hectares, and frequently is much less (Stepanov, 1939; Dal', 1941; Meladze, 1947; Kostyuchenko, 1950; Lavrov, 1957; Trushchalova, 1959; Aliev, 1962 and others). In Kazakhstan and Kirghizia, the density is even lower but in small sections, for example, along the shore of Lake Issyk-Kul', the raccoon dog population reaches 20–25 animals per 1000 hectares (Berens and Yanushevich, 1956 and others).

Habitat. In the Far East, preferred habitat of the raccoon dog is light deciduous and mixed forests near streams with dense understory, or the thick growths of shrubs, usually found on gentle slopes of mountains, interrupted by waterfalls and creeks, with rock outcrops and clear areas. In southern Ussuri territory, more than half of all encounters with raccoon dogs, their burrows and excrements, were found in rare oak-hornbeam forests with ground cover of rhododendron, honeysuckle and other bushes. They avoid coniferous forests and are only encountered there along forest edges, riparian shrubs, or on cliffs along the sea coast. In unforested regions, they are met with only in stands of reeds along the shore of rivers and lakes. They usually live at an elevation of up to 100–300 m above sea level, rarely up to 600–700 m (Bannikov, 1964).

In the central zone of the European part of the USSR, they prefer deciduous and mixed forests of flood plains, and avoid dense coniferous tracts and extensive open bogs and fields. At the northwest, the main sites of the raccoon dog consist of southern taiga forest (30% of occurrences in summer and 49.5% in winter), shores of water bodies (26 and 20.8% respectively), bogs (12.7 and 10.2%), clearcuts and burns (11.3 and 7.1%); in this, mixed forests adjacent to floodplain sections of the meadows and fields provide the principal sites both in winter and in summer (Geller, 1959). In Novgorod district in flooded forests, the number of raccoon dogs is 13; in grassy fir groves, 8; in pine woods, 1–3 animals per 1000 hectares (Morozov, 1948). In Tatariya in forests,



77 Fig. 24. Reedgrass and sedge meadows in the lowland of Lake Khanka (southern Primor'e). Biotope of raccoon dog. Photograph by A.G. Pankrat'ev.

raccoon dog encounter frequency is 33% (from 25 in summer to 40–60% in winter and spring), in floodplains—30% (56% in summer, 10–19% in winter and spring), in ravines with bushes—11.5%, in bogs—6.2%, in fields—14.4% (Yu. Popov, 1956). In Voronezh district, they prefer to live in deciduous and mixed forests, especially on floodplains where nearly half of all litters were noted; in small glades in boggy depressions (more than 1/3 of the litters counted); in large tracts of pine, they are confined to forest edges, in burns and clearcuts (Obtemperanskii, 1953). In Gor'kovsk district, they prefer the floodplain deciduous forests with rich stands of grass (Kozlov, 1952). In 78 Byelorussia its favorite habitat is broad-leaved and mixed forest islands, the copses among meadows and small bogs with dense undergrowth of hazel, buckthorn and other bushes, and also dense growths of alder thickets and oiser-beds along the banks of rivers and lakes; it decidedly avoids dry pine woods (Dol'bik, 1952).

In Ukraine, it prefers the floodplains with growths of oiser and high grass as well as the edges of bogs and flood-pools in the lower reaches of large rivers. It establishes itself on river-terrace forests of aspen and alder or in oak-groves, especially with dense understory. In winter it does not abandon river floodplains (Korneev, 1954). In the Donbass, besides floodplains, it willingly colonizes ravines overgrown



77 Fig. 25. Biotope of raccoon dog—Borzi river valley in its lower reaches, Amursk district. Photograph by A.G. Pankrat'ev.

with shrubs, and in small shrubs in the steppes (Sakhno, 1948). In Rostov district, it lives among shrubs, in ravines and depressions as well as in growths of reeds (Rall', Kritskaya, 1958). On the shore of the Azov Sea, it is found in reed thickets and in growths of shrubs (Kostyunchenko, 1950). Similar places are inhabited by this species along the shore of the Caspian Sea and in the Volga delta. In the northern Caucasus, the raccoon dog lives along the banks of rivers, lakes and creeks, in ravines and gullies overgrown with bushes, in isolated oak-groves among the steppes and in broad-leaved and mixed montane forests. In the belt of montane coniferous forests, they are encountered half as often as in mixed and broad-leaved forests (Trushchalova, 1959). In Georgia, this species is confined to cut-over forests and shrublands along river banks (Meladze, 1947); in Kirghizia, they live along swampy shores of lakes, rivulets and in berry-bushes and reeds (Berens, Yanushevich, 1956). The raccoon dog was introduced into Siberia, but quickly died out; it inhabited forested floodplains of rivers where nut-pine is found and shrubs are abundant; in summer, they frequently occupied open nut-pine woods in searching for food (Nadeev, 1940).

Apparently, mixed and deciduous forests, alternating with small open areas near water, represent the most favorable habitat of the

raccoon dog in its natural range, as well as in places where it has been successfully acclimatized. In the majority of northern and central regions of acclimatization, the raccoon dog prefers, in the snowy period of the year, to live in open places (fields, meadows, marshes) where it can move easily.

Food. According to the constituents of its food, the raccoon dog is an omnivorous animal. The following morphological characteristics attest to its omnivory: weak development of canines and carnassial teeth, flat surface of molar teeth, and relatively long intestine (1.5–2 times longer than that of other species in the family). The diversity of food objects is very great. Animal food appeared in all stomachs and feces, while plant food was, on the average, 64%.

Among animal foods, the most significant frequency of appearance (in %) in all seasons and regions on the average are:

Insects	47 (maximum, to 93)
Mouse-like rodents	46–(85)
Amphibians	18–(65)
Birds	13–(23)
Fish	9–(24)
Reptiles	8–(36)
Molluscs	7–(47)
Carrion	6–(13)
Insectivores	5–(14)

The absolute significance of one or another food is not only in terms of frequency but also volume. In total, the role of mouse-like rodents is considerably greater than that of insects. For example, the frequency of occurrence of mouse-like rodents and insects in the food of the raccoon dog of Voronezh preserve constitutes 60 and 46% respectively. The volume of food ("food coefficient"—the product of the number of occurrences multiplied by the volume in percentage, divided by 100) for mouse-like rodents is equal to 58, and for insects—18 (Ivanova, 1962). In all regions inhabited by the raccoon dog, it may be confirmed that mouse-like rodents occupy the first place in the nutrition of the species. The significance of other food groups is very variable and depending on the season and the conditions of the regions, insects or amphibians, birds or plant food constitute the food base. In one way or other, all the above-mentioned food groups are always the main component of raccoon dog food.

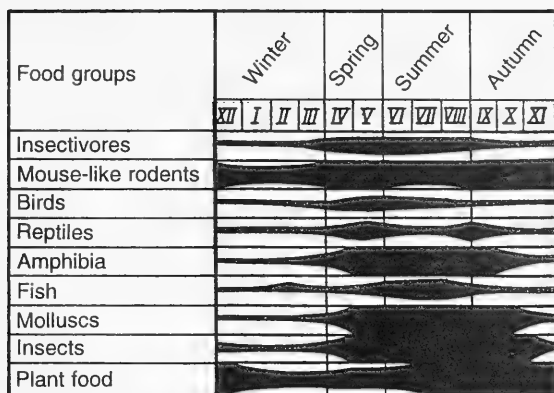


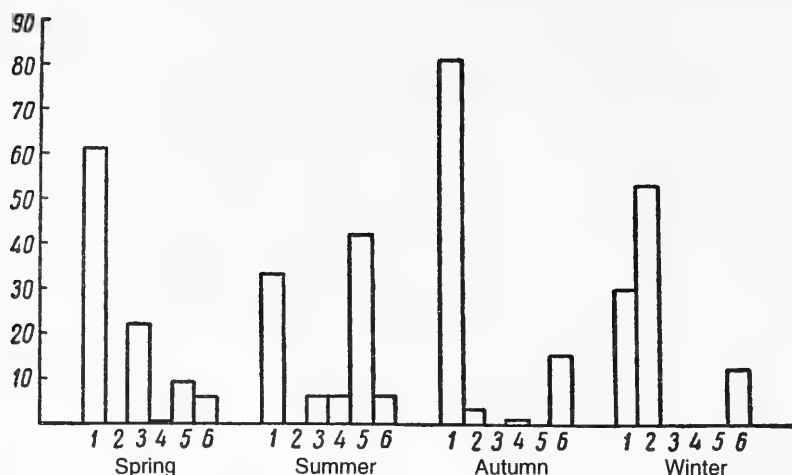
Fig. 26. Change in food of the raccoon dog by seasons (from Yu. Popov, 1956).

Mouse-like rodents in the food of the raccoon dog are mainly represented by voles. Among the latter, those species living in damp brushy undergrowth, banks of water bodies and coppices are more frequent than other species; these are: reed voles, root voles, water voles, common voles and others. In forest regions, the beasts rarely feed on common redbacked voles. Mice are 5–10 times rarer than voles; as an exception (in Astrakhan district) gerbils are of great importance in the nutrition of raccoon dog.

Insects constituting the food of the raccoon dog are more frequently represented by: dung beetles, cockchafers or water beetles and water scavenger beetles; other groups are more rarely found: tiger and ground beetles, carrion beetles, grasshoppers and others. Frogs are more common than the other amphibia among the food of raccoon dog. In some instances, for example in Voronezh region, fire-bellied toads [*Bombina*] were the usual food (Ivanova, 1962), while in the Ukraine, their usual food was the spade-foot toad [*Pelobates*] (Korneev, 1954).

Among birds in the stomachs and feces of raccoon dog, the most frequent are the remains of either ducks or passeriform birds; commonly passeriforms nesting in the area (buntings, pipits, warblers and others) or else migrant species—thrushes, jays, etc. Where there are colonies of nesting terns and gulls, their eggs and nestlings are common food of raccoon dog. In the northern regions of raccoon dog acclimatization, grouse are usually its prey (Sorokin, 1956). In the Ussuri territory, cases of destruction of pheasant nests were recorded.

The raccoon dog usually utilizes only large fish which are cast up in spring after freezing; it rarely catches fish in passage during the spawning migration. In Primor'e, it usually collects fish and inverte-

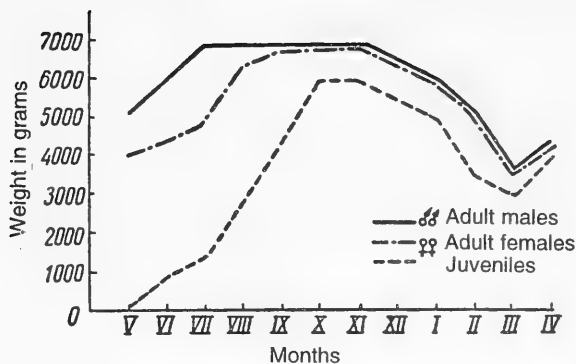


79 Fig. 27. Seasonal variation of food groups in the nutrition of raccoon dog (in food-units) (from Ivanova, 1962).
1—Mouse-like rodents; 2—Carrion; 3—Birds; 4—Amphibia; 5—Insects; 6—Plant food.



80 Fig. 28. Raccoon dog searching for food on river ice. "Kedrovaya Pad'" preserve, southern Primor'e. March 1964. Photograph by A.G. Pankrat'ev.

brates on the sea shore. It catches small fish from water bodies drying out in summer. Snakes are the more frequent prey among reptilians. Lizards are 2–3 times rarer. In the southern regions of their acclimatization, the raccoon dog willingly catches young tortoises and digs out the clutches of tortoise eggs (Rukovskii, 1950). Both water molluscs—



80 Fig. 29. Change in weight of the raccoon dog during the year (after Yu. Popov, 1956).

bivalves, pond snails and flat-coiled snails—and land snails are included in the food of raccoon dogs.

Among insectivorous animals, the usual prey are shrews and hedgehogs, rarely moles and desmans. In the Far East, the Ussuri mole [*Mogera robusta*] is the usual prey of raccoon dog, a fact which is probably determined by the surface position of its feeding burrows.

Plant food is also highly variable. It may be the vegetative parts of plants, bulbs, rhizomes, grains of agricultural crops (most frequent are oats, millet, maize), nuts, fruits, berries, grapes, melons, watermelons, pumpkins, tomatoes, etc. In Ussuri territory, the most important are fruits of wild fruit trees, Amur cork trees, acorns and wild grapes. Fruits of [cultivated] fruit trees and grapes have a great importance in the feeding of the raccoon dogs acclimatized in the southern regions. In the northern regions oats, berries (bilberry, cranberry, strawberry, and others) and the vegetative parts of plants play a great role.

81 The fairly evident seasonal change in the food of the raccoon dog is greatly determined by the different availability of these or other food items during the year. Thus in late autumn and winter, mouse-like rodents appear to be the main food of the raccoon dog, or in the north it might be carrion and feces; since amphibians, reptiles, molluscs and insects disappear. In the southern regions, the most important food items are the grains of agricultural crops, fruits, and also those amphibia not undergoing hibernation (Korneev, 1954; Trushchalova, 1959 and others).

In spring, especially during snow melt, the number of mouse-like rodents available to the raccoon dog sharply increase because of the poor protection afforded by their burrows. During this period, amphibians play also their greatest role. During the flight period of cockchafers and the reproduction of dung beetles in the late spring, these insects are also shown to be main foods. Vegetative parts of plants are very important. In summer the food is most diverse and, besides mouse-like rodents, the relative role of which decreases, birds are of great importance (especially in the nesting period). Insects are important, and fish, reptilians and molluscs are found more frequently than in other seasons. By the end of summer, a greater role is taken by berries, grains, fruits and vegetables.

In autumn, plant food is the most important item in comparison to all other seasons. In connection with the increase in the number of mouse-like rodents, their role increases, but the insects, amphibians, reptiles and birds gradually disappear from the food ration (Table 1).

82 The importance of one or another food group differs remarkably according to the year. Thus, in the food of raccoon dog, the frequency of occurrence of the main food group—mouse-like rodents—may change nearly two-fold (Table 2). The decrease in the role of mouse-like rodents in the food (determined by the drop in their number) entails a sharp increase in the significance of birds, amphibians and insectivores. In other instances, the lack of mouse-like rodents is compensated by the intensive eating of carrion (Novgorodsk and Kalininsk districts; Geller, 1959), feces (Tatariya; Yu. Popov, 1956), or fruits (Caucasus; Trushchalova, 1959). Parallel to the decrease in the role of mouse-like rodents in the food of the raccoon dog, the general significance of plant food also decreases.

The food contributions of animals inhabiting different places also vary somewhat. Thus, mouse-like rodents (common voles) are highly important in the food of raccoon dog litters at the forest edges in Voronezh preserve. Because of the low number of mouse-like rodents within the forest, their importance in the food of litters living in the center of the forest was very low; the deficiency of rodents here is compensated by amphibians and insects (Table 3). The food of litters living in floodplains was more diverse; the most important were waterfowl (Ivanova, 1962). Differences nearly as sharp as these in the food components of raccoon dogs inhabiting various biotopes were noted in Tatariya (Yu. Popov, 1956), in Belorussia (Samusenko and Golodushko, 1961) and in other regions.

81

Table 1. Seasonal change in raccoon dog food in Primor'e (E.P. Spangenberg) and in the northwestern European part of the USSR (frequency, %; Geller, 1959)

Type of food	Region, season, number of data	Primor'e territory		Northwestern USSR	
		Spring and summer, 97	Autumn, 26	Spring and summer, 214	Autumn, 130
<i>Animals</i>					
Insectivores		—	—	5.6	7.5
Mouse-like rodents		18.6	15.4	17.7	48.3
Birds and their eggs		8.3	—	16.8	4.1
Lizards		7.2	—	—	—
Snakes		4.2	—	Trace	—
Turtle eggs		5.2	—	—	—
Amphibia		65.5	15.4	52.8	19.1
Fish		18.6	23.0	1.3	10.0
Insects		32.0	23.0	1.3	10.0
Molluscs		47.3	11.3	Trace	10.0
Carriion		2.1	—	6.5	15.8
Feces		—	—	5.7	1.6
<i>Plants</i>					
Nuts and grains		11.3	11.3	—	—
Grass		26.8	46.1	57.2	—
Oat		—	—	3.7	68.3
Rice		4.2	—	—	—
Polygonum, millet, corn		2.1	19.2	—	—
Berries		2.6	—	6.6	10.7
Grapes		—	46.1	—	—
Apples		—	62.2	—	—
Cork tree		—	61.5	—	—
Acorns		—	—	—	5.0

The sharp differences in the importance of one or another food in different seasons in various years and in various habitats make it difficult to establish rules governing the variability of food components (Tables 1, 2, and 3a).

In northern and middle latitudes, mouse-like rodents occupy first place among animal food; in the south and west—insects. As one moves southward, the role of birds and molluscs increases. Naturally, geographic variability of food includes replacement of some food types by others within one food group (different species of mouse-like

Table 2. Change in importance of foods of raccoon dog in various years (frequency of occurrence, %)

Type of food \ Region, author, year	Voronezhsk district (Ivanova, 1962)		Tatariya (Yu. Popov, 1956)		Northwestern European part of USSR (Morozov, 1956; Geller, 1959)	
	1958	1959	1949	1950	1941	1947
Insectivores	5.4	15.0	No data		0.9	6.9
Mouse-like rodents	74.6	49.7	59.3	76.0	40.3	22.3
Birds	13.5	33.2	No data		4.3	10.2
Reptiles	2.2	3.2	No data		—	—
Amphibians	12.4	23.7	14.1	6.5	11.9	29.8
Insects	48.6	43.9	56.0	53.0	29.8	7.6
Plants	50.8	40.8	40.3	28.6	94.7	34.0

rodents, insects, berries and so on in different regions). The extremely scanty material for the feeding of raccoon dog in the Far East does not permit any [comparative] analysis of changes in food components of acclimatized animals [elsewhere] [the changes mentioned by Geller (1959) are confined to annual and seasonal variability of feeding].

Home range. Data about the size of the home range are almost absent. The distance between the inhabited burrows, which may serve as an indirect indication of the size of the home range, is extremely variable. The burrows may be separated from each other by some kilometers or (as in Primor'e and on Askol'd Island) very close to each other. Burrows were distributed in colonies consisting of 4–5 (up to 10) each in Rostovsk district where the foraging area of the raccoon dog reaches 10 km² (Stepanov, 1939; Rall' and Kritskaya, 1953).

In the northwestern regions of acclimatization, judging by 19 tracks, the length of the daily travel of the raccoon dog is equal to 3–6 km in winter, in early spring 15–20 km, in late spring 6–8 km, in summer 6–10 km, in early autumn 8–12 km, and in late autumn 2–3 km. The area within which these travels take place, was equal to 1 to 12 km² (Geller, 1959). In Tatariya, the length of the daily travel of the animals in search of food in early spring reaches a maximum of 10–14 km; in summer, when food is abundant, this travel is less and the radius of activity of seven raccoon dogs consisted of 600–800 m. In autumn, when fat is accumulating, the length of the foraging circuit may reach 8 km, but usually is 4–6 km. In winter, during periods of thaw, they

82 **Table 3. Foods of raccoon dog litters in different habitats in Voronezh Preserve (frequency of occurrence, %)**

Type of food \ Biotope	Floodplain (burrow No. 1)	Forest (burrow No. 2)	Forest edge (burrow No. 3)
Mouse-like rodents	25.7	5.0	56.0
Birds	48.6	—	20.0
Reptiles	8.6	10.0	8.0
Amphibians	31.4	70.0	16.0
Insects	62.8	100.0	52.0
Plants	25.7	20.0	56.0

do not go further than 100–150 m away from shelter (Yu. Popov, 1956).

Burrows and shelters. Raccoon dogs use several types of shelters: beds and lairs in open areas, and burrows, both temporary and permanent ones (breeding and wintering dens).

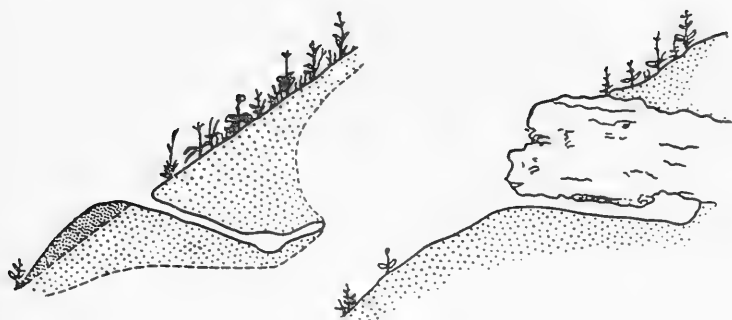
In the Ussuri territory, summer beds are generally places on dry slopes under a protective rock, boulders or in brushy undergrowth. In the Khankaish lowland, beds/nests found in September–October were between hummocks on a thick (4.5–6 cm) layer of accumulated cuttings of dry sedge, reed and other grassy vegetation. At the bottom of the nest, scraps of wool were found. The internal diameter of such nests is 84 78–100 cm, the depth is 32–36 cm. Around the nest the reeds usually form an obstruction by arching above the nest. In the Ussuri territory, beds are found in the depressions between roots of old trees and in the spacious hollows of fallen lime trees [*Tilia*].

Based on investigation of 49 burrows in the Ussuri territory, the majority of the holes are located 500–800 m away from the banks of water bodies, most frequently (41%) at eastern points of the compass. Slopes on which burrows were found were covered with forests (88%) or shrubs (12%). 78% of the burrows were found under piles of stones, 12% in loose soil, 8% in rock niches, and 2% under tree-roots (Bannikov and Sergeev, 1939).

The horizontal diameter of the passage of burrows beneath stones is often equal to 24–29 cm (21 to 31 cm), vertical diameter 20–24 cm (20 to 34 cm). In the burrow there are usually 1–2 entrance holes, in some instances 3–5. The longest passage to the nesting cavity is 2 m, more frequently 1.5 m, i.e., the burrows of this type are comparatively short and simply constructed. The nesting cavity has a flat bottom and a dome-shaped roof; its dimensions are 50–70 × 30–45 cm.

Table 3a. Frequency (%) of the main food groups in the nutrition of raccoon dog in different regions of the USSR

Food group	Region											
	Voronezhsk district											
Mouse-like rodents	50.8	52.7	41.3	80.9	74.4	26.4	60.4	85.3	48.2	45.2	30.2	55.3
Insects	20.9	29.8	54.1	50.7	52.0	44.6	46.5	41.0	66.8	57.1	93.4	66.2
Amphibians	19.9	9.5	35.3	7.1	12.8	4.5	17	1.8	37.0	8.4	10.3	0.7
Birds	9.2	4.3	15.0	10.4	7.9	2.2	23.0	16.1	16.9	18.0	16.9	18.4
Fish	1.4	0.36	0.7	1.6	1.9	0.7	—	5.0	7.8	8.1	15.0	—
Reptiles	1.0	2.4	3.0	6.9	2.9	2.6	3.5	—	21.4	3.2	35.8	4.4
Molluscs	0.5	—	3.0	1.5	1.4	1.8	0.6	2.7	7.4	—	3.7	9.1
Carrion	5.7	2.6	—	—	4.8	0.3	3.8	5.4	0.8	—	—	12.4
Insectivores	3.6	0.93	18.8	—	1.1	1.9	13.2	2.7	1.2	2.9	—	13.3
Plants	24.7	94.7	27.7	42.5	24.4	68.9	44.2	38.0	53.5	No data	44.3	65.0
												Northern Caucasus (Trushchalova, 1959), 515 samples
												Astrakhansk district (Rukovskii, 1950), 106 samples
												Manychsk steppe (Kritskaya, 1961), 283 samples
												Ukraine (Korneev, 1954), 500 samples
												Okskii Preserve (Borodin, 1951), 224 samples
												Ivanova (1962), 636 samples
												Obtemperanskii (1952), 1600 samples
												Tatariya (Yu. Popov, 1956), 2694 samples
												Byelorussia (Samusenko and Golodushko, 1961), 505 samples
												Lithuania (Prusaitė, 1960), 133 samples
												Novgorodsk and Leningradsk districts (Morozov, 1947), 1066 samples
												Kaliningrad district (Sorokin, 1956), 578 samples

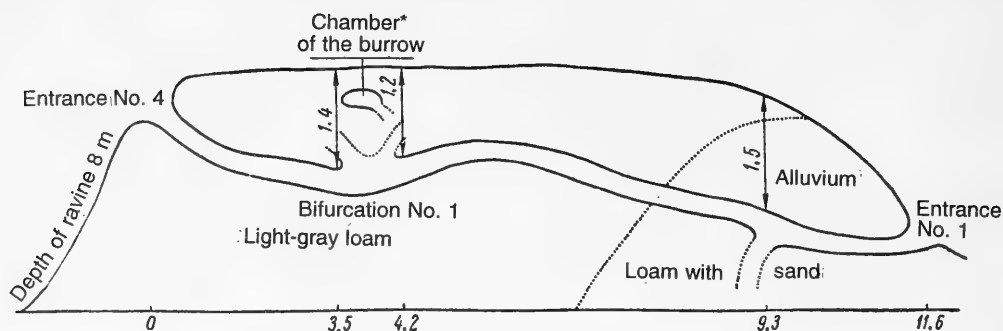


84 Fig. 30. Burrows of raccoon dog. Scheme of location and cross section (after Bannikov and Sergeev, 1939).

Most often (36 burrows out of 38) there is only one entrance to the cavity; the side burrows join together in front of the nesting cavity in one principal passage. The bottom of the cavity is usually lined with different dry plant remains, leaves of hazel, oak, maple, lespedeza, stems and leaves of grasses and herbs.

Near the burrow, usually not farther than 10–15 m, and in the burrows with litters, toilets in the form of pits are located, sometimes directly near the entrance, filled with excrements. Near the burrow under piles of stones occur latrines in the form of numerous heaps of excrements on flat rocks. In such cases, the latrine is frequently located 20–30 m, or farther, from the burrow.

85 Burrows excavated in soft ground in Ussuri territory were situated along the slopes of river valleys, in places poor in rock outcrops. They are quite simple, having 1–3 exits averaging 21×24 cm in diameter ($18\text{--}22 \times 25\text{--}29$ cm). Fan-shaped scattered soil and gravel are found in front of the entrance to the hole and lower along the slope. The burrow passage usually passes downward directly into the ground without any turns at an angle of $20\text{--}25^\circ$; its length reaches 6 m (most frequently 3 m) and ends with a nesting chamber which does not essentially differ from that described above in burrows under stones, but in the holes dug in soft ground, the layer of leaf and grass bedding is less. In some burrows a blind side hole proceeds from the nesting chamber which sometimes rises slightly upwards, in which the concealed animal is found when the burrow is dug up. Burrows in rock niches are only accessible for external inspection. There is one entrance to such burrows; wide fissures (more than 50 cm) and those opening upwards are not occupied by raccoon dogs (a burrow located under the roots of an old lime tree had 3 entrance openings under the tree).



84

Fig. 31. Scheme of construction of raccoon dog burrow (from Yu. Popov, 1956).

*In Russian original *kotel*, which means "caldron, boiler, pot"—Sci. Ed.

Shelters of the raccoon dog in places of their acclimatization are similar to those described. In Tatariya and Rostovsk district, summer beds, in the form of small holes without bedding are situated on dry places at the base of slanting shrubs growing in depressions, and the shores of marshes and lakes (Rall' and Kritskaya, 1953; Yu. Popov, 1956). The raccoon dog sometimes constructs a lair in tall, dense sedge thickets in the form of a plaza (70 × 100 cm) on small piles of mowed sedge or other grass remaining from the previous year. In Tatariya, winter lairs on the frozen swamps in dense growths of reed and cattail (Yu. Popov, 1956) resemble lairs in the Khankaish lowland. Raccoon dogs accumulate the dry sedge to serve as bedding, while the surrounding high grasses bend under the weight of the snow forming an arch above the lair. Below it the animals construct a whole labyrinth of hidden passages, ending in an outlet on the surface of the snow cover, sometimes 15–20 cm away from the lair. Such lairs constituted in Tatariya more than 37% of all aboveground shelters.

In many regions of acclimatization, typical lairs are under haystacks and shocks. Such dens are usually also used in winter or for whelping; they are situated under tangled fallen trees, under stones, in old sheds, in trenches, in dug-outs, and in entrenchments remaining after the war. In such dens, there is bedding of dry grasses and leaves. Shelters in the hollows of fallen trees or in hollows located at ground level are quite frequent. Thus, in the northwestern European part of USSR, 17% of winter dens of raccoon dog were found under the roots of trees, 13%—in dug-outs, 10%—in entrenchments, 3%—in hollows and stacks (Geller, 1959). In Tatariya, 5.9% of the lairs were found in hollows (burrows not included)—4.8% under haystacks and 5.3%—in heaps of dry branches (Yu. Popov, 1956).

The significance of burrows as shelters for the raccoon dog in places of acclimatization may be highly variable even in neighboring regions. Thus, in Voronezhsk district, about 75% of the litters of the raccoon dog were found in burrows (Obtemperanskii, 1952), in Voronezh Preserve—more than 86% (Ivanova, 1962). In the latter, old burrows of badgers and red foxes are especially numerous, and the ground is sandy. In the northwestern regions, about 50% of the raccoon dogs occupy burrows (Geller, 1959); in the Ukraine, they rarely utilize burrows (Korneev, 1954), but in Rostovsk district they live, as a rule, in burrows (Rall' and Kritskaya, 1953).

The raccoon dog usually hurries to occupy the old burrows of badgers and red foxes, and digs itself a new burrow only when there are no free ones. In Tatariya, 77.8% of the burrows occupied by the raccoon dog were old ones of badgers (38.6%) or of red foxes (39.2%) (Yu. Popov, 1956). The same phenomenon was observed in other regions. In using the burrows of badgers and foxes, the raccoon dog, as a rule, does not dig additional side burrows and does not construct a new nesting chamber, but only brings in dry bedding, throwing away the rotted. On occupying the complicated holes of badgers, the raccoon dog uses 2–3 side burrows and the others are neglected.

86 Many cases of wintering of raccoon dog and badger in one hole have been recorded. This is possible, because the badger enters into hibernation at least 2 weeks earlier than the raccoon dog and leaves the burrows 2 weeks after the raccoon dog. In the event that the raccoon dog remains longer in the burrow, the badger drives it away and not rarely bites it to death (Korneev, 1954; Geller, 1959; Ivanova, 1962 and others). Exceptionally, cases of cohabitation of litters of badger and raccoon dog in one burrow are known (Tikhvinskii, 1938; Yu. Popov, 1956 and others).

In those cases, when the raccoon dog itself digs, it constructs temporary as well as permanent burrows. Temporary burrows are simple in construction, small and short (length to 1 m), always with a single entrance hole. The animals dig them in soft ground, often under bushes or young pine trees, usually on precipitous slopes, along river banks, at forest edges and in fields. Permanent littering and wintering burrows are more frequently dug on the slopes of forest ravines, in floodplains of rivers and at the borders of bogs, not far from forest edges or openings in the forest and often on elevated parts of watersheds. In this case, preference is shown for deciduous and mixed forests of various

species, with a rich forest understory. The nature of the ground is not, apparently, of decisive importance, but sandy soils are preferred.

Proper burrows in Voronezh Preserve had one entrance hole in 57.1% of cases, two in 25% and more than 2 entrance holes in only 18% (Ivanova, 1959). This relationship of burrows with various numbers of passages is also found in other regions. The general length of the burrow ranges from 1.5 to 5 m, often 2.5–3 m. A chamber 40–50 cm in diameter is situated at a depth of 60–90 cm (usually 70–75 cm). Width of the entrance hole exceeds its height, its dimensions being 24×29 cm (from 19 to 41 cm). One passage usually leads to the chamber; as an exception, blind side holes occur, proceeding 60–80 cm away from the chamber. The floor of the chamber is lined with a small layer of bedding made of dry grass and leaves.

At the burrow, soil thrown out in a fan shape over 1.5–1.8 m occurs. The dug-out soil and the area around the burrow are trampled down by the animals, and evident traces of their thin claws are usually seen on the walls of the burrow. 5–10 m, but sometimes 2–3 m, from the burrow is located a latrine with pits. The trails of the animals are seen on the discarded soil but these paths are narrow (not exceeding 20 cm), and this distinguishes the holes of raccoon dog from those of foxes, the paths of which are broad (25–35 cm) at the burrow, and the excavated soil coming from the hole is rounded in shape. The burrow of the raccoon dog differs from those of the badger in that the soil thrown from the hole of the latter is elongated, and the trails are not usually seen, since all the excavated soil is trampled down by the feet of the animals (Yu. Popov, 1956; Ivanova, 1959, 1962 and others).

The raccoon dog, apparently, changes the shelters seasonally. Thus, in Tatariya, the beasts overwinter in burrows, dens or winter beds. With increased activity in March, they often start to use temporary burrows or beds, but at the end of April, before whelping, they again occupy permanent holes, throwing out the old bedding from them and bringing in new. By the middle of June, when the pups are about one month old, the animals leave the littering shelters and use temporary summer shelters, only rarely visiting the burrows. In autumn, visits to the permanent holes become frequent, and in the middle of October, the animals clean them a second time and change the bedding; at the end of October, they finally settle in their winter shelters (Yu. Popov, 1956).

Daily activity and behavior. The raccoon dog is a nocturnal and crepuscular animal. However, in the short nights of summer, activity

occurs during sunny periods in the morning and evening hours. During the day, activity of the animals is curtailed and they hide in shelters or spend the time bedded down. During the period of rut, pregnancy and the initiation of nursing the young, from March to May, the raccoon dogs are very cautious and are active almost exclusively in the dark period of the 24 hours. In summer, when the pups begin to feed independently, they frequently are encountered during the daytime. In autumn, in September, regardless of increased feeding, raccoon dogs rarely come out in the daytime and usually leave their shelters only at twilight. In winter, the animals are active at twilight and during the night.

Upon leaving the burrow the raccoon dog in search of food follows the shore of the nearest water body. It frequently goes into water and wanders along the shallows.

On the sea coast, along shores of lakes and rivers, at dawn and in the evening, it is almost always possible to see feeding animals. In the forest the raccoon dog moves slowly, looking under every bush, pile and stump. Only when crossing openings does it move at a quick trot. The raccoon dog is cautious but in case of danger it does not run away, but conceals itself, camouflaging itself very skillfully. If they are overtaken, some animals (in the Far East) pretend to be dead, but on the first opportunity, they run away and conceal themselves nearby. The entire litter usually grows fat together at the end of summer. It is possible to observe two or three adult animals, feeding in immediate proximity to one another.

Having comparatively short legs, the raccoon dog, in the presence of a snow cover 10–12 cm deep, already stops “dragging”, and searches for food with difficulty. In a snow depth of more than 20 cm deep or deeper the animals move with great difficulty, “swimming” in the snow. The weight load for the track is relatively great: in December it is 75–80 g/cm², in March 33–37 g/cm² (Yu. Popov, 1956). The sense of smell is very sharp, and hearing and vision are more weakly developed than in closely-related species.

Hibernation, winter sleep. True winter torpor, i.e. deep uninterrupted sleep, associated with a sharp fall in metabolic level and body temperature, is not observed in the raccoon dog. However, the general metabolism may decrease by about 25% (Sokolov, 1949).

In warm winters in the Ussuri territory, as well as in places of acclimatization (Ukraine; Korneev, 1954), the beasts do not go into hibernation during the course of the entire winter and only during snowstorms they do not go out of their shelters for some days. Usually

in December, when the snow cover reaches 15–20 cm, the activity of the raccoon dogs sharply decreases and they leave their shelter for a short time only on warm, quiet days and they do not go farther from the burrow than 150–200 m. From February to the beginning of March, the activity of the animal again sharply increases, both from food deficiency as well as the beginning of rut, and this period leads to an increase in the movements of the raccoon dog. During spring snowfalls (March–April) the animals again may go into shelter for some days.

At the beginning of the winter period, the raccoon dog puts on an average of 18–23% of subcutaneous and 3–5% of internal fat (of total weight). Animals putting on less than this amount (though often gaining) as a rule remain wandering and rarely survive the winter. During the first years of acclimatization, when animals were not yet sufficiently adapted to catching the local food, as a result of this they exhibited weak fattening in autumn, and frequently did not hibernate (Obtemperanskii, 1958 and others). Low temperature exerts little influence on the activity of the raccoon dog. Instances are known of animals being encountered at -20 to -25°C .

Raccoon dogs kept in artificial burrows in hutches fell into hibernation in December, but aroused and fed during a time of warming; in the period of rut (in mid-February) they wandered about, but then at several times hibernated again (Obtemperanskii, 1958). Confirmation of partial winter activity of the raccoon dog is attested by their being caught by hunters. Thus, in Tatariya, about 80% of the animals are caught from November to January and 20% from the 1st of January to the 15th of February (Yu. Popov, 1956). In the northwest of the country, about 37% of the animals are caught in December, in January—28% and in February—18% (Geller, 1959).

88 *Seasonal migrations and transgressions.* The raccoon dog is a sedentary animal, and regular seasonal migrations are not known for this species.

In the Ussuri territory, hunters have reported migrations of raccoon dogs in unfavorable years. In the Lake Khanka depression, massive migration of the animals to China seemed to have been observed in the autumn of 1929 when, within a few days, up to one hundred animals were seen moving in one direction. Such migrations are doubtful; probably what occurs is the migration in the winter of a small number of animals living during the summer in reeds from flooded depressions to dry places.



Fig. 32. A young raccoon dog, just appearing after winter sleep. "Kedrovaya Pad" preserve, southern Primor'e. 17 February 1965. Photograph by A.G. Pankrat'ev.

After releases in new regions, there were migrations of individual animals for 20–80 km from the place where they were originally introduced (Rall' and Kritskaya, 1953; Trushchalova, 1959 and others). There is the possibility of more distant migrations, since intrusions of the animals onto the tundra have been recorded (Skrobov, 1958). An emigration of about 600 km was recorded in Ukraine (Korneev, 1954). The greatest migrations of the raccoon dog are recorded in floodplains; during the final spring floodwaters, females with litters move up to divides.

Reproduction. Rut is observed from the beginning of February to the end of April depending upon the region and climatic conditions. Later spring may delay the beginning of rut for 2–3 weeks. The return of cold weather, and especially snowfalls, usually interrupt rut. In the Ussuri territory, rut takes place on the average in the middle of March, but it often is delayed until the end of March or beginning of April. In the Ukraine, in Voronezhsk district and Tatariya, rut occurs in the middle of February (Korneev, 1954; Yu. Popov, 1956; Obtemperanskii,

1958); in the northwest, in the beginning or middle of March (Geller, 1959 and others). Rut continues for 2–3 weeks, but in captivity, it is usually not less than 3 weeks, and often 26–28 days, and during food shortage, up to 40 days (Pavlinskii, 1937).

Raccoon dogs are monogamous animals and pairs are formed even in autumn, usually in October or November. Fights among males occur occasionally at the time of rut, are brief and not violent, and are
89 accompanied by yelping and hollow growling. In captivity, polygamy is possible when one male is in contact with 4–5 females. Copulation occurs most frequently during the night or early in the morning, usually in quiet weather. Coitus lasts for 6–9 minutes on the average (from 2 to 26 minutes). Estrus in females continues from several hours to 6 days and during this period they mate up to 5 times, usually 2–3. After 20–24 days, estrus is repeated even in pregnant females (Petryaev and Khatkevitch, 1931; Pavlinskii, 1937).

Pregnancy lasts 61–70 days (often 59 days [*sic*]*). Young are born in April, but mostly in May. Cases are known when the main mass of births is delayed until June, and in a few cases newborn have been found as late as September.

In the Far East, the litter mostly consists of 6–7 young, but their number may reach 15–16 (Firsov, 1929; Przheval'skii, 1870**). The size of the litter in the regions of acclimatization fluctuates greatly, in connection, probably, with fluctuation of conditions in various years. Thus, in Voronezhsk district (Obtemperanskii, 1958) average litter size was 4.9 pups (from 4.3 to 5.75 in different years); in the northwestern districts in 1938–1939—5.2; in 1947—5.9; in 1946–1949 average, 6.3 (Morozov, 1953; Geller, 1959). In Tatariya (Yu. Popov, 1956) the average litter size was 7.3 pups; in the Ukraine (Korneev, 1954)—7.9 (to 16 pups); in Lithuania—from 4 to 13, average, 9.5 (Prusaite, 1961). The average occurring in captivity is 7.1 pups (Petryaev and Khatkevitch, 1931). Females giving birth to pups for the first time have smaller litters than females of older age, and their litters are 1 or 2 pups fewer. The ratio of sexes at birth is nearly 1 : 1; but males are somewhat more frequent. Thus, in Tatariya (Yu. Popov, 1956) litters contained 50.9% males and 49.1% females; in the northwest (Geller, 1959)—51.7% and 48.3% respectively; and in Voronezhsk district (Obtemperanskii, 1958)—58.7% and 41.3%. In State animal farms (Pavlinskii, 1939)—52% males and 48% females.

*Russian original inconsistent—Sci. Ed.

**In Russian original, 1947 (not in Lit. Cit.)—Sci. Ed.

Barrenness of females in different regions of acclimatization constitutes about 12% (Yu. Popov, 1956; Geller, 1959 and others). In captivity, after one mounting [by male] 30.9% of the females remain non-pregnant and after three mountings, practically no females are barren (Starkov, 1940). The male takes an active part in raising the young. In Tatariya the average number of pups in the litter decreases from 7.3 in May to 5.9 in June due to mortality (Yu. Popov, 1956). Juvenile mortality increases in June when the pups leave the shelter (at an age of 25–30 days), and reaches its maximum in July and August when the growing pups separate from the litter. The litter finally breaks up at the end of August–September, and in October juveniles, reaching the size of adults, unite in pairs. During this period about 35% of the young have died, and each pair of adults during this time produces 4 juveniles (Morozov, 1953). By September and October, about 50% of the young have died (Geller, 1959).

Growth, development, and molt. Young are born blind, covered with short, dense, soft wool, without guard hairs, of dark-slaty, nearly black color. Weight of newborn, 60–110 g. Males weigh 5–10% more than females. Eyes open on the 9th–10th day. On the 14th–16th days teeth erupt—beginning with the upper canines, then the incisors and lower canines. Approximately from the age of 10 days, guard hairs begin to grow on the hips and shoulders, and then near the ears and on the cheeks. The dark color of the pup gradually becomes gray, starting with the abdomen, 2 weeks after birth. Guard hairs start to grow especially quickly at the age of 1.5–2 months when the black or blackish-brown color prevailing in the color of pups quickly changes to gray. The black tones remain only around the eyes. On all the interorbital area, from the forehead to the nose, the brown color of the underfur also changes into light gray. By this time, as a result of lengthening of hairs on the cheeks, “side-whiskers” begin to form. In 3-month-old
90 pups, the guard hairs are shorter than those of adults only on the chest, chin, tail and distal parts of the extremities.

Lactation lasts for 45–60 days, but from 3 weeks or one month of age, the pups start eating frogs, insects and other food brought to them by the parents. At the age of 1 month, the pups weigh 550–650 g; at 2 months, 1100–1300 g; 3 months, 2500–2900 g; and at 4 months — about 4 kg. At an age of 4.5–5 months, young attain the weight and size of adults and are almost not different from them in color (Pavlinskii, 1937; Korneev, 1954; Yu. Popov, 1956; Geller, 1959 and others).

The lowest weight of adults is attained in March (about 3 kg). By

August—beginning of September, males reach their greatest weight—6.5–7 kg (certain individuals, 9–10 kg). Females deposit fat reserves more slowly and maximum weight is usually attained one or one and a half months later than males, i.e. by September–October. Juveniles attain greatest weight another month later than females—in October–November. In autumn, fat constitutes 30–35% of live weight of the animals and forms a subcutaneous layer up to 1.5 cm (Yu. Popov, 1956; Geller, 1959).

Sexual maturity is attained at an age of 8–10 months. The duration of life is not known. In nature, individuals older than 6–7 years are encountered. In captivity, animals are known to have lived to 11 years.

The age composition of populations is insufficiently studied. In the northwestern regions, juveniles constituted 53.8% of the population in the hunting season and animals of older ages—46.2% (Geller, 1959). Among animals caught in Tatariya in the hunting season, juveniles constitute 57.2% of the population, adults—42.8% (among them, 19% are older than 1 year, 11.3% older than 2 years, 6.7% older than 3 years, 3.9% older than 4 years, 1.9% older than 5 years). In Lithuania in 1957–1959, one-year-old animals constituted 67.5% of the population (Prusaite, 1961).

Molt occurs only once a year—in spring. Shedding of the underfur starts in February–March depending upon the region, coming of spring, and condition of the animals. Shedding of underfur starts on the neck and withers; then molt extends to the shoulders, back, sides and the posterior part of the body. By the middle of May–June (and July in the northern regions), guard hair almost alone remains on the skin, and the fur acquires a dark color because of the proximity of the tips of the guard hairs, which have black tips. From June onward, guard hairs are gradually replaced and the underwool starts growing. Renewal of the latter takes place slowly compared with guard hair, and therefore the pelage attains normal development from the last days of October, to November, and even December. The underfur (new) per 1 cm² of the rump is in August—2072, in October—6264, and in December—9624 (Trushchalova, 1959). In old males, molt takes place more quickly than in females and juveniles (Korneev, 1954; Morozova, 1955; Geller, 1959 and others).

Enemies, diseases, parasites, mortality, competitors and population dynamics. Among the enemies of the raccoon dog, the most important is the wolf. It destroys raccoon dogs early in spring—in February–March, and also in summer. However attacks on raccoon dogs by

wolves have been noted in late autumn also. Stray dogs destroy mainly the growing pups. Apparently, during the period of litter dissolution, red foxes also destroy pups. Instances are known of foxes biting raccoon dogs to death (see below).

In Tatariya, out of the 54 recorded cases of death of raccoon dogs by predators, 55.6% of the animals were killed by wolves, 27.8%—by stray dogs, 11.1%—by red foxes, 3.7%—by the golden eagle and 1.8%—by the eagle-owl [*Bubo bubo*] (Yu. Popov, 1956). In the north-western regions, out of the 186 recorded cases of death of raccoon dogs by predators, 64% were attributed to the wolf, 14.3%—to fox, 12.8%—to stray dogs, 6.3%—to lynx and 2.6%—to birds of prey (Geller, 91 1959). Lynx, because of its low numbers, causes little damage to the raccoon dog, as observed in the majority of regions; still more rarely do brown bears attack raccoon dogs. Among birds of prey involved in attacks, usually on pups, are golden eagle, white-tailed eagle [*Haliaeetus albicilla*], goshawk and eagle-owl.

Among the raccoon dogs' competitors, fox and badger are the most important, since foxes play a role with raccoon dogs in feeding on mouse-like rodents, whereas the badger generally shares with them feeding on insects and plants. However in the summer period, thanks to the abundance of food, the various habitats and different methods of hunting, there is no sharp competition among these species of predators. This competition becomes somewhat sharper in early spring (February, March), in the most difficult period of the year. Competition with foxes and badgers for burrows is practically absent, for the raccoon dog is entirely unassuming in its struggle for shelter (see above). However, individual cases have been recorded, when badger or fox killed the raccoon dog which had occupied its burrow.

The parasitic fauna of raccoon dogs was investigated in the Far East (Shpringol'ts-Shmidt, 1935; Petrov, 1941), in State animal farms (Gusev, 1951; Savinov, 1953 and others), in Tatariya (Yu. Popov, 1956), in the Ukraine (Korneev, 1954), in the northwestern regions (Antipin, 1946; Morozov, 1953; Savinov, 1953; Geller, 1959), in the northern Caucasus (Trushchalova, 1959), in the lower Volga region (Sviridov, 1952), and in Lithuania (Prusaite, 1961).

In all, 32 species of parasitic worms are known from the raccoon dog: 8 species of trematodes (*Opisthorchis felineus*, *Clonorchis sinensis*, *Pseudamphistomum truncatum*, *Euparyphium melis*, *Metagonimus yokogawai*, *Plagiorchis massino*, *Alaria alata*, *Paragonimus westermani*), 7 species of cestodes (*Diphyllbothrium mansonii*,

Taenia hydatigena, *T. polyacantha*, *Multiceps multiceps*, *M. serialis*, *Diphylidium caninum*, *Mesocestoides lineatus*) and 17 species of nematodes (*Ascaris columnaris*, *Toxascaris leonina*, *T[oxocara] canis*, *Capillaria yamaguti*, *C. plica*, *C. putori*, *Thominx aerophilus*, *Ancylostoma caninum*, *Uncinaria stenocephala*, *Molineus patans*, *Crenosoma vulpis*, *Diectophyma renale*, *Physaloptera sibirica*, *Thelazia callipaeda*, *Strongyloides erschowi*, *Trichinella spiralis*, *Macracanthorhynchus catulinum**).

In the Far East, 18 species of parasitic worms were found in raccoon dogs, and 12 species were found in regions of acclimatization. Such species as *Clonorchis sinensis*, *Metagonimus yokogawai*, *Paragonimus westermani* were not found in acclimatized animals due to the absence of their intermediate hosts in Europe—the Eastern molluscs. Some species: *Opisthorchis felineus*, *Plagiorchis massino*, *Taenia hydatigena*, *T. polyacantha*, *Multiceps multiceps*, *M. serialis*, *Ascaris columnaris*, *Ancylostoma caninum* were acquired by raccoon dogs during the process of acclimatization.

In the northwestern regions there has been noted a high degree of infection (up to 96% and 10–20 parasites per 1 cm² of small intestine) with the trematode *Alaria alata*; somewhat less (33.7%)—with the nematode *Uncinaria stenocephala* (Savinov, 1953; Geller, 1959). In Tatariya, a great number of animals were found to be infected by *Alaria alata*, but the total number of infected animals was less (76.2%) than in the northwest (Yu. Popov, 1956), in Lithuania, a lesser number of animals (54%) was infected by this parasite (Prusaite, 1961). In the Ukraine, 3 species of parasitic worms were found, including *Alaria alata* in 33.3% of animals. Infection with *Alaria* takes place through frogs infected with the metacercaria** of *Alaria*. In the Caucasus (Trushchalova, 1959) a considerable number (27.9%) of raccoon dogs are infected with the ascarid *Ascaris columnaris*. 9.3% of raccoon dogs of Lithuania (Prusaite, 1961) are infected with the larvae of *Trichinella spiralis*. However, the pathogenic significance of parasitic worms to raccoon dogs is little studied. In Kievsk district in 1952, there was massive mortality among raccoon dogs due to bronchopneumonia of a trematode nature (Korneev, 1954).

92 Six species of fleas have been found on raccoon dogs: *Chaetopsylla trichosa*, *C. globiceps*, *Paraceras melis*, *Ctenocephalides canis*,

*an acanthocephalan; misspellings in Russian original have been corrected—Sci. Ed.

**Actually, mesocercaria—Sci. Ed.

C. felis, *Pulex irritans*, as well as chewing lice, Mallophaga; 5 species of ticks: *Dermacentor pictus*, *Ixodes ricinus*, *I. persulcatus*, *I. crenulatus* and the causative agent of mange—*Acarus siro**. The latter is fairly widespread in the Ukraine, Voronezhsk district, Lithuania and a series of other regions, causing massive outbreaks of mange. Raccoon dogs are strongly infected with the biting louse *Trichodectes canis*; in the State animal farms of the Far East, this parasite afflicts up to 90% of animals (Shpringol'ts-Shmidt, 1935) causing a marked exhaustion of the animals.

Diseases of the raccoon dog are poorly studied. Cases of rabies were recorded in the lower Volga (Isakov, 1949), Voronezhsk district (Obtemperanskii, 1958), Lithuania (Prusaite, 1961) and in other regions. In the Ukraine (Sakhno, 1948; Korneev, 1954) and in Tatariya (Tikhvinskii, 1938) cases of massive epizootics of piroplasmosis were recorded. In the northern Caucasus, epizootic carnivore distemper was noted among raccoon dogs (Trushchalova, 1959); a known case of a raccoon dog ill with leptospirosis (N.N. Rukovskii); in State animal farms, carnivore plague, paratyphoid, anthrax, and tuberculosis sickness (Burov, Buzinov, Bannovskii, Lyubashchenko and others, 1939).

Epizootics may be an important factor in reducing the number of raccoon dogs. "An almost complete destruction of the whole stock" was observed as a result of an epizootic of piroplasmosis in Kievsk and Chernigovsk districts (Korneev, 1954) and in Tatariya (Tikhvinskii, 1937). A great number of raccoon dogs are lost to mange, which, however, does not lead to a massive die-off of the animals, as is known for foxes (Prusaite, 1961 and others). The number of raccoon dogs may be sharply reduced as a result of mortality from rabies (Isakov, 1949).

Among the abiotic factors which cause a sharp decrease in the number of raccoon dogs, the spring flooding which coincides with the period of reproduction is important. At that time, young die in the dens; and, apparently, a significant number of pregnant females are killed (Korneev, 1954 and others). In the northern regions, a cause of reduction in numbers may be spring snowfall, involving lack of food, death due to predators, increase in the number of non-pregnant females and lowering of fertility (Yu. Popov, 1956; Obtemperanskii, 1958; Geller, 1959 and others). There are no concrete data about the magnitude of mortality due to different causes. In the flooded areas of the Dnepr, Volga and other large rivers, in some years the greater part of population is killed. However, in favorable years, due to the high fertility

*Mange is also caused by *Sarcoptes*—Sci. Ed.

(see above) the population doubles by autumn, and the number of raccoon dog is quickly restored.

The number of raccoon dog is related to food availability. Thus, in Voronezhsk district, 3–4 fold fluctuations in the number of this carnivore were observed. The fall and rise in the numbers is related to changes in the numbers of the principal food—mouse-like rodents—in the preceding year and has a 3–4-year cycle (Ivanova, 1962).

Field characteristics. A stocky animal of medium size, on short legs, with small head and pointed muzzle; ears almost hidden in thick fur and typical “side-whiskers” on the cheeks.

When in danger, conceals itself, closely presses itself to the ground and, owing to its brown color, merges with the surrounding soil background or forest bedding. In case of direct close approach of a human, it usually closes its eyes and lies completely still, even when touched. During twilight and night, it is more courageous and sometimes tries to defend itself. It swims well, willingly enters water and can swim across wide rivers and lakes.

In the places inhabited by raccoon dogs, holes dug in search of insects may be found. These holes are 5–15 cm in depth and are



Fig. 33. Prints of front and hind paws of raccoon dog in silt. On the right, scheme of the usual position of tracks during slow movement. Volga delta, 24 August 1943. Sketch by A.N. Formozov, about 2/3 natural size.

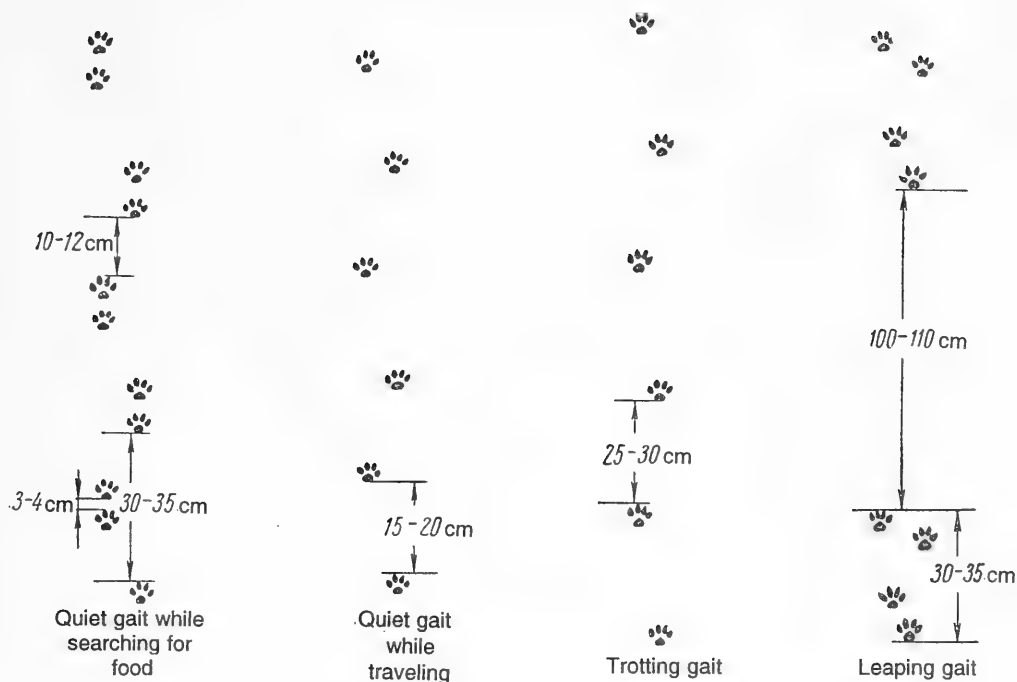


Fig. 34. Tracks of raccoon dog during various gaits (from Yu. Popov, 1956).

reminiscent of badgers, but usually wider. A fan of excavated soil (see above) is typical of the burrow.

Tracks are rounded in form, nearly 5×5 cm for the front, and 4.5×5 cm for the hind feet. As a rule, the prints of their claws are generally easily seen. Unlike foxes, the series of tracks of the running raccoon dog is not straight, but zig-zag. A raccoon dog when fattening walks slowly, and looks in each pool, hole and under bushes and stumps; moving in this way, the tracks of the hind paws do not reach the tracks of the front. Having short legs they leave "drags" [marks] and "eyes" [holes] on the snow when it is 10 cm deep. In the snow cover depth of 25-30 cm, the animal leaves a deep furrow in the loose snow.

Typical "latrines" in the form of heaps of excrement are found in definite places, usually 10-15 cm from the den or on trails. Unlike badgers, the raccoon dog does not bury or hide its excrement. Feces are 40-60 mm in length and 20-30 diameter and are composed of 2-3 pieces.

Usually silent; only in the rutting period, the males yelp and give a hollow growl. (A.B.).

Practical Significance

The raccoon dog provides thick, long, strong, but coarse fur. When cage reared, the animals also provided about 100 g of wool, of a quality somewhat inferior to that of goats. In a series of regions in the Far East, the meat of raccoon dog is used by the local inhabitants as food. Analysis of the meat (18% protein, 3% fat; more than 4186.8 joules/kg¹⁰) reveals its high nutritious qualities (Korneev, 1954).

Data about the size of the catch in the past are almost lacking. In the eighties of the past century, the trade of raccoon dog in the Primor'e and Ussuri territories was "quite developed" (Silant'ev, 1898) and occupied an evident place in the fur trade (Nadarov, 1888). The world harvest in its entire range, including Japan, North and South Korea and China in 1907–1910 comprised 260–300 thousand pelts (Kaplin and others, 1955); of which, judging by indirect data, about 5–8%, i.e. 15–20 thousand pelts were obtained from Russia. These figures are, apparently, exaggerated, for the production of the whole fur industry in the Russian Far East was estimated at about 40 thousand rubles, and hunting in these regions included sable, red fox, otter, Kolonok, wolverine, bear, wolf, tiger and others. Even if we suppose that the raccoon dog furs constituted 50% of this value (which is hardly probable), then, if the price of raccoon dog fur is 2 rubles, their number would not exceed 10,000. Probably, the total catch was 5–6 thousand pelts.

In the 30's, when lands were considerably opened up, about 12 thousand raccoon dogs were caught.

In the regions of acclimatization licensed trade started in 1948–1950, and the licensed restrictions were removed in 1953–1955. After the start of the trade, the number of animals harvested sharply increased, and from 1953 to 1961, it fluctuated within 30–70 thousand pelts. For example, in 1955, about 41 thousand were obtained, and in 1961–66 thousand. In the latter year, of these about 10 thousand were obtained from natural habitat in the Far East, and 56 thousand from places of acclimatization. Of these 56 thousand, Byelorussia provided 6.5 thousand pelts, the Ukraine—about 5 thousand, Latvia, Lithuania

¹⁰According to international energy system (SI).

and Krasnodarsk territory—4 thousand each, Kalininsk district—3.7 thousand, Pskovsk—2.7 thousand, Astrakhansk—2.3 thousand, Vologodsk, Moskovsk, Leningradsk, Novgorodsk, Smolensk, and Yaroslavsk districts, Azerbaidzhan, Estonia, and Dagestan—from 1 to 2 thousand pelts each. In the remaining districts, territories and republics, the annual catch was less than one thousand pelts.

Everywhere the raccoon dog is hunted from November until the snow is deep, i.e. usually until February. In the Far East, the main way of hunting the raccoon dog is by tracking with *laikas* or mongrel dogs at night. In the past century, the Gol'dy* and Orocheny* also hunted by night with dogs on whose necks were fastened small bells. Less frequently, they hunted with different "devices" (Nadarov, 1888 and others). In places of acclimatization, methods of hunting raccoon dogs are also simple. In the majority of cases, it is hunted incidentally while hunting other fur animals or specifically harvested with the help of dogs. With dogs, 80–90% of the animals, on average, are caught; with
95 guns, 8–10%; with traps, 5–7%. The dog quickly follows the trail and overtakes the animal, and if it does not flee into a burrow, the dog strangles it or worries it until the hunter arrives. Traps for the raccoon dogs are put at burrows, along the shores of water bodies, and around marshes and ponds.

Cage rearing of raccoon dogs started in the Far East in 1928 (Firsov, 1929). In 1934 there were 15 State farms where the animal was raised. Collective fur farms in the first year of their existence selected the raccoon dog as their principal object.

Later, the captive population in the collective fur farms began to decrease because the raccoon dog requires nearly the same food as needed by the silver fox. By the end of the 30's and the beginning of the 40's, the breeding of raccoon dog was broadly developed only in the collective farms of the Ukraine and from 1945 on, this type of fur husbandry started to decrease (Il'ina, 1952 and others).

In the 30's work began on acclimatizing this animal in the European part of USSR, in the Caucasus, and in Siberia. From 1928 to 1958 about 10 thousand individuals were introduced in 76 districts, territories and republics. The first attempts at transplantation started in the Primor'e territory where the raccoon dog was brought to some islands in the Japanese sea. In 1934, it was introduced into the Altai, northern Caucasus, in Armenia, Kirgizia, Tatariya, Kalininsk, Penzensk and

*Indigenous tribes in the Far East—Sci. Ed.

Orenburgsk districts. In the following year—into Leningradsk, Murmansk, and Novosibirsk districts, Bashkiriya and other regions. The raccoon dog was most intensively transplanted in 1936 when more than 1,200 beasts were introduced, and then from 1948 to 1953, when 500–800 individuals were introduced every year in tens of districts (Shaposhnikov, 1956; Lavrov, 1957 and others).

The acclimatization of raccoon dogs in Irkutsk and Novosibirsk districts, in Trans-Baikaliya and the Altai did not give results due to severe winters and inadequate diet. The raccoon dogs acclimatized poorly in the montane regions of the Caucasus, Trans-Caucasus, Middle Asia and in Moldavia (Meladze, 1947; Yanushevich, 1956; Arens, 1957; Trushchalova, 1959 and others). Success followed the introduction of raccoon dog into the European part of USSR, especially in the northwest (Pribaltic, Byelorussia, Kalininsk, Novgorodsk, Pskovsk, Smolensk districts), in the central regions (Moskovsk, Yaroslavsk, Vologodsk, Gorkovsk, Vladimirsk, Ryazansk and other districts), as well as in the chernozem [black soil] belt (Voronezhsk, Tambovsk, Kursk districts), the lower Volga region and the level parts of the northern Caucasus and Dagestan. In the Ukraine, the greatest number of raccoon dog was established in Poltavsk, Khersonsk and Lugansk districts.

The trade quality of fur of the raccoon dog acclimatized in the northwest was somewhat improved. Thus, in Kalininsk district (Morozov, 1955; Sorokin, 1956) raccoon dog fur became somewhat denser and softer. The length of the guard and top hairs increased by 7.96% on the average, that of the under fur, by 5.3%. The thickness of the guard and top hair decreased by 3.41%. The density of the fur increased by 11.3%. The fur color became somewhat darker; the darkest "black-brown" color in Kalininsk district is found in 8% of the beasts against 3% in their homeland* (Morozov, 1951, 1955; Tserevitinov, 1953).

The importance of the raccoon dog in the hunting economy of a series of regions is not yet sufficiently clear. Thus, the importance of this animal is not clear in the Far East. The raccoon dog causes appreciable damage to the pheasant by destroying its nests; this is hardly compensated by the benefit gained from its destruction of harmful rodents and insects. In regions of acclimatization the harmful activity of the raccoon dog in the hunting economy, agriculture and also public health is obvious. Cases of nest destruction and eating of birds and

*Probably refers to indigenous animals in the Far East—Sci. Ed.

96 nestlings of waterfowl and marsh birds are numerous (Korneev, 1954). The harm caused by the raccoon dog in floodlands and shores of estuaries is especially sensitive, since, in spring, it feeds entirely on the eggs and nestlings of waterfowl. In the floodlands of the Oka river, raccoon dogs destroy a great number of wild fowl; about 46% of its food consists of birds (Borodin, 1951). In the Voronezh preserve, birds constitute 48.6% of the food of the raccoon dog litters inhabiting the floodlands. Moreover, the raccoon dog destroys a considerable number of birds (45%) during the time of spring migration (Ivanov, 1962). In Lithuania, birds constitute 15–20% of raccoon dog food and this carnivore causes noticeable damage to waterfowl and forest game (Prusaite, 1960, 1961). The raccoon dog frequently destroys muskrat houses and eats their young (Korneev, 1954; Kritskaya, 1961).

In the Ukraine and in many other southern regions, the raccoon dog causes harm to kitchen garden and melon cultivation, vineyards and corn seedlings (Korneev, 1954, and others). Evidently the raccoon dog plays a negative role as a carrier of rabies, piroplasmosis and scabies (see above).

A series of authors (Obtemperanskii, 1956; Yu. Popov, 1956; Sorokin, 1957; Samusenko and Golodushko, 1961), on the basis of the fact that rodents and insects constitute the main food of raccoon dog while birds are of secondary importance in its food, consider the harm caused by these beasts to be negligible. However, the destruction of up to 90% of the broods of waterfowl (Korneev, 1954) or of a considerable number of the broods of forest game and small passerine birds is hardly compensated by the destruction of mouse-like rodents in the warm period of year. Undoubtedly, in a series of regions, the harm caused by the raccoon dog may be relatively small, and in others very great, and this requires concrete analysis; however, as a whole, damage by the raccoon dog to the hunting economy is evident.

In spite of the fact that as a result of acclimatization, the preparation of raccoon dog pelts grew 4–6 times and in a series of districts and republics its specific contribution to fur production constitutes up to 10–30%, the interests of the protection of nature and sport hunting economy require the destruction of raccoon dog in places where it has become acclimatized (A.B.).

GENUS OF WOLVES

Genus *Canis* Linnaeus, 1758

1758. *Canis*. Linnaeus. Syst. Naturae. Ed. X, I, p. 38. *Canis familiaris* = *Canis lupus* L. (domestic dog)¹.
 1816. *Thos*. Oken. Lehrb. d. Naturg., 3, Th. 2, p. 1037. *Thos vulgaris* Oken = *Canis aureus* Linnaeus.
 1816. *Lupus*. Oken. Ibid., p. 1039. *Canis lupus* Linnaeus.
 1857. *Vulpicanis*. Blainville. Ann. Sc. Nat. Paris, Zool., 8; pt. 2, p. 279. *Canis aureus* Linnaeus.
 1839. *Sacalius*. H. Smith. Jardine's Naturalists Library, Mamm., 25, p. 214. *Sacalius aureus* = *Canis aureus* Linnaeus.
 1841. *Oxygous*. Hodgson. Calcutta Journ. Nat. Hist., 2, p. 213. *Canis aureus* Linnaeus.

Large species, but in part of moderate size.

- Skull broad and massive, with moderately diverging zygomatic arches, high (height in the occipital region more than 1/3 of condylobasal length), in adults and old animals well-developed crests, in particular, a large sagittal crest. Facial parts of the skull relatively weakly elongated, massive, quite high, and always longer than the cranial parts (distance from the posterior margin of the infraorbital foramen to the posterior margin of the canine alveolus is less than or equal to the skull width above the canines; distance from the line joining the tips of the supraorbital processes to the anterior end of the premaxillae is greater than that to the upper part of the occipital condyle). Interorbital (frontal) region convex with large cavities (sinuses) and is clearly and quite abruptly elevated above the line of the dorsal profile of rostrum. Supraorbital processes, which also have cavities, are not large in area, but massive, and their upper surface is convex, the tip summit bent somewhat downwards, and without sharp borders (edges). Posterior margin of tooth row extends to the level of the anterior margin of the interpterygoid fossa. Deep notch on posterior lower margin of lower jaw anterior to angular process absent.

Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42$. Teeth large and massive,

¹As was shown (see vol. I, p. 540), in this book domestic forms are excluded from the nomenclature. The wolf, *C. lupus*, must therefore be considered the generic type, not only as the most typical species of the genus but also as the ancestral form of "*C. familiaris*."

carnassial teeth strongly manifested, palatal length about 2.5 times length of upper carnassial tooth (P^4) and cheek teeth. Canines slightly curved, massive, broad at base and relatively short. When jaws are closed, tips of upper canines do not reach middle of mandible, while tips of lower [canines] do not, or only just, reach margins of alveoli of upper canines. Tips of upper canines directed straight downwards; no pronounced longitudinal sharp ridge on posterior side of canine, surface of canine smooth. Cutting edges of incisors with small accessory lateral cusps (trilobed).

In general appearance, the animals are long-legged, with noticeably elongated trunk; tail is fluffy, of moderate length—up to two-thirds length of trunk with the head (often less) and not more than twice as long as hind limbs. When the animal is standing, its end is usually not lower or only slightly lower than the tarsal joint, but it never reaches the ground.

Head notably elongated with somewhat pointed muzzle or else blunter or fairly broad with broad forehead. Ears relatively short with pointed tips. On sole of hind foot, behind four naked digital pads is situated a larger fifth. Pads of digits III and IV of fore limbs either separate or united (jackal, Fig. 17).

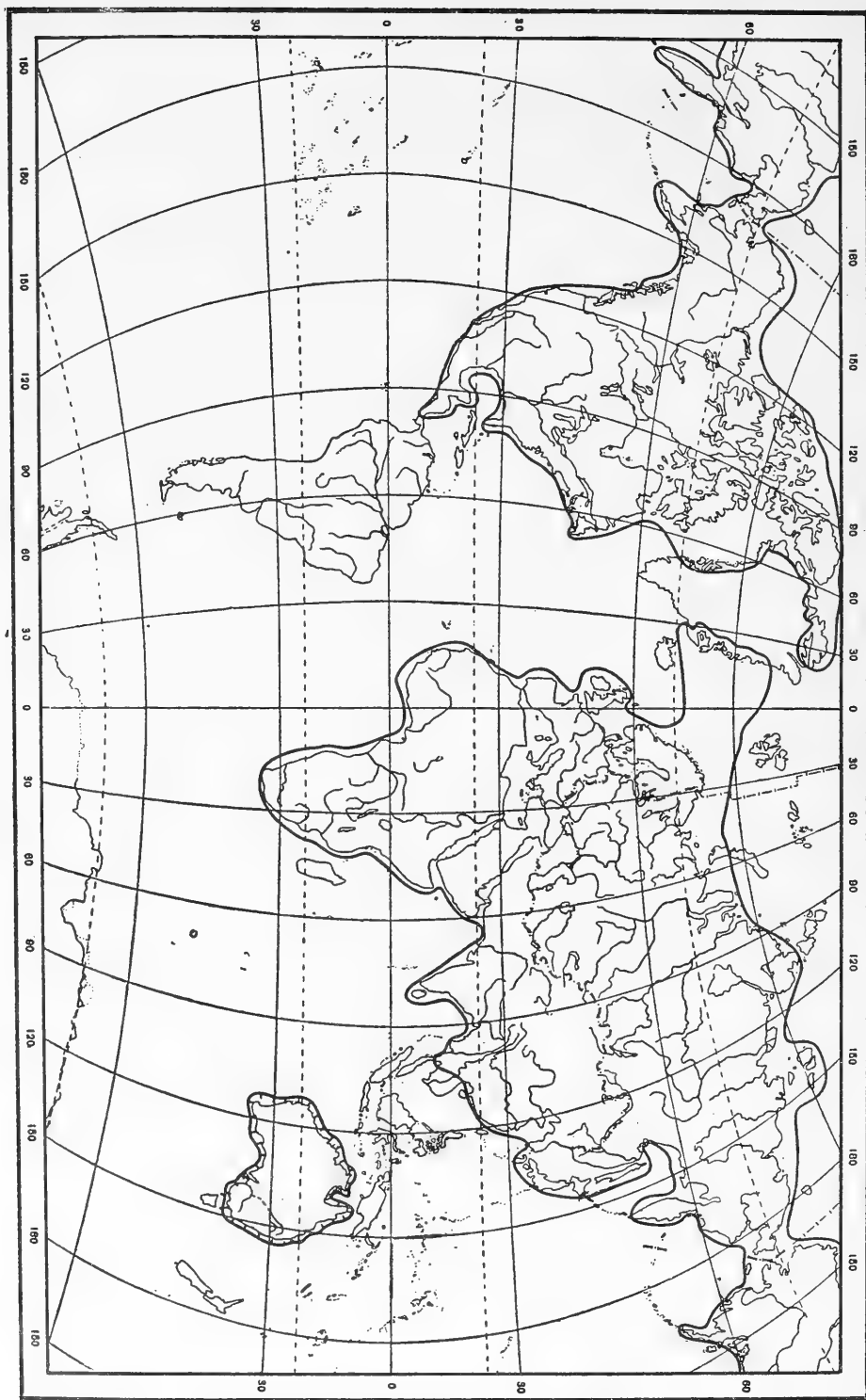
Fur quite coarse. Color unimorphic (dimorphic only in some races of wolf, *C. lupus*, from southern North America—“*C. niger*”), grayish, yellowish, and reddish tones mixed with black hairs, sometimes with noticeable black dorsal saddle; adult animals never exclusively monotone (except black phase of “*C. niger*”). Violaceous* gland present, but weakly developed. Teats usually 5 pairs.

Sharp sexual dimorphism absent, but females are usually somewhat smaller than males. Age dimorphism occurs, and seasonal [dimorphism] is well marked in some species, but manifested almost only in density and length of fur. Two molts per year.

Species of the genus are very close to each other and homogeneous, representing the wolf type—the true gray wolf (*C. lupus*) and its small copy—the jackal. The large forms of the wolf have the greatest dimensions (see family characteristics, and below—description of wolf), the smallest jackals are not more than 80–90 cm in body length, usually about 70–75 cm, and in weight not more than 10–12 kg, usually about 6–7 kg.

Species of the genus are found in all landscapes from tundra to lowlands of hot deserts, and high mountains. They prefer regions with

*Also called supracaudal—Sci. Ed.



98 Fig. 35. Reconstructed range of the genus of wolves, *Canis* L. The line surrounding Australia outlines the range of the dingo ("*Canis dingo*"). (V.G. Heptner).

more or less open areas and abundant wild or domestic hoofed mammals. They are sedentary, [but] individual animals sometimes roam widely and settle in distant areas. Monogamous animals; moreover, some form close pairs for several years. 10–13 pups, usually less. Young usually delivered in open den. Predators, feeding mainly on the meat of mammals, frequently large ones (ungulates), in part on carrion
 99 and other vertebrates, exceptionally on invertebrates, and at times even plants. Except during breeding, they usually live and hunt in small groups. In some species, internal relationships in the group (rank, etc.) are sharply marked (wolves), in others, quite weakly (jackals).

This genus is very widely distributed, extending in the north to the northernmost points of land (83°20' N. Lat.—not found on floating ice); also found in equatorial regions. In the New World, it occupies the entire continent of North America (including the entire Arctic archipelago) and in the south, it extends to Costa Rica inclusive. It is absent on the Queen Charlotte Islands and islands of the Bering Sea. In Greenland, it occupies the northern, eastern and western coasts, southward nearly to 70° N. Lat.

In the Old World, its range occupies all of Africa (excluding Madagascar) and all of Eurasia southward to southern China, Siam [Thailand], Burma, Assam and Ceylon inclusive. In the north, the range includes the Kolguev Islands [Barents Sea], south island of Novaya Zemlya, Belyi [island] adjacent to the Taimyr coast, as well as Lyakhovskii Islands and the New Siberian archipelago. They are also found in Kamchatka, Sakhalin and the Japanese islands. They are absent on Iceland, Spitsbergen, Franz Josef Land, Severnaya Zemlya, Wrangel Island, the Commander Islands, the majority of the Kuril islands and Shantar Island, Taiwan, Hainan, and the Malacca and Malaya archipelago.² At the present time, it is exterminated in a series of territories of North America, in the greater part of West and Central Europe, in part of Japan and in several other places. This genus represents a highly adaptable and viable group, and its range has decreased only in the regions of dense human population and where it has been directly persecuted to extinction.

The genus appeared in the upper Pliocene of North America; in Eurasia, in the Pleistocene (see characteristics of genus *Vulpes*).

Particular generic or subgeneric names have been proposed for almost every species included in the genus of contents accepted here. This occurred during the period of narrow interpretation of the species

²A feral domestic dog—“*Canis dingo*”—is found in a completely wild condition in Australia (except Tasmania).

concept, when many of the races were considered to be separate species, and these [genera or subgenera] could be group names. At the present time, there is no basis for dividing the genus into several subgenera, and it is senseless to separate, within it, such subgenera as *Canis* for the wolf and *Thos*, *Schaeffia*, *Lupulella* for the various forms of jackals. The differences between these "subgenera" are very insignificant; moreover, in the present species concept, only one species is included in each subgenus. Division of the genus into two subgenera: *Canis* and *Thos*, i.e. wolf and jackal is also not justified. In some respects, the species of the genus themselves represent the fullest and most characteristic expression of the family type.

This genus is most closely related to the group *Simenia* (Abyssinian wolf) and *Vulpes* (foxes) and especially to *Alopex* (arctic fox). This latter represents, in craniological respects, a quite clear transition and connecting link between *Canis* and *Vulpes*. In the past, all these groups, especially *Canis*, *Vulpes* and *Alopex*, were usually grouped in one genus or were considered as subgenera only. Later, however, all authors essentially divided these groups generically or, at least, separated *Canis* from *Vulpes*, united *Alopex* with the latter group, and separated *Simenia*. Most recently, it was again proposed (Haltenorth, 1958) that all the mentioned groups including a series of others be considered members of one enlarged genus—*Canis* (see characteristics of the family). In this account, the described groups occupy subgeneric positions. This point of view deserves consideration, but requires broader argument.

In the genus are 5 species: 2 African—*C. adustus* (striped jackal) and *C. mesomelas* (shabrack [= black-backed] jackal), 1 North American—*C. latrans* (coyote), 1 Eurasiatic-African—*C. aureus* (jackal) and 1 Eurasiatic-North American—*C. lupus* (wolf).³ The species of this genus constitute about 17% of the species of the family.

One species—the wolf—is found both in the wild and in the domestic state as the domestic dog ("*Canis familiaris*"). The dog—the most strongly altered form as compared to its wild ancestor—is generally the most strongly divergent and diverse of domestic animals (the number of breeds exceeds 200). Nevertheless, in respect to the wolf, there is no reproductive isolation. The view which was widespread not long ago, concerning the diphyletic origin of the domestic dog—from wolf and jackal—is now totally disregarded. As in other domestic animals, the dog has one original species ("ancestor"). The possibility of the diphyletic origin of the dog is excluded

³The wolf of Florida and the southeastern states adjacent to the Mississippi [River], is considered by American authors to be a separate species—*C. niger*.

in particular by the difference in the diploid number of chromosomes—78 in wolf and dog and 74 in jackal (Matthey, 1954).

In the USSR, two species are found: wolf, *Canis lupus* Linnaeus, 1758 and jackal, *Canis aureus* Linnaeus 1758—about 40% of the species of the genus and about 0.6% of the number of mammals of the Union.

The range of the genus covers the entire territory of the USSR, except the above-mentioned northern territories and islands.

The species of the genus are of great importance in the USSR as pests of livestock and the hunting economy and, to a lesser extent, as carriers of rabies. Their importance as fur-bearing species is not great and less than the harm they cause (V.H.).

JACKAL, CHEKALKA

Canis aureus Linnaeus, 1758

- 1758. *Canis aureus* Linnaeus. Syst. nat. Ed. X, 1, p. 40. Laristan, southern Iran.
- 1835. *Canis aureus* var. *moreotica*. Geoffroy. Exped. Scient. de Moree, Zool., pl. 1. Peloponnesus (Morea), Greece.
- 1858. *Canis aureus* typicus oder var. *caucasica*. Kolenati. Reiseerinnerungen. Th. I, p. 96, Armenia. (V.H.).

Diagnosis

Adult body length not more than 90 cm, tail length about one-third of body length. Length of skull less than 200 mm. Arciform line formed by anterior border of both nasal bones has, in the middle (along suture between nasal bones), a well-marked projection, directed anteriorly. At antero-internal sides of auditory bullae, swellings in form of ridges on basioccipital absent. Cingulum on outer surface of first upper molar well marked, broad and continuous (Figs. 15, 16). (V.H.).

Description

In its general appearance, the jackal is very similar to the wolf, but much smaller in size, lighter in weight, with shorter legs and with a somewhat more elongated trunk and shorter tail. Its end just reaches the heel or a bit below it. As in the wolf, the tail always droops. The head

is lighter, not so "foreheaded"* , and the muzzle is narrower and more pointed. On the whole, the jackal much resembles a small mongrel dog. Fur is coarse and stiff. Iris is light or dark brownish. Teats 5 pairs.

General color of winter fur is dirty reddish-gray, strongly highlighted with blackish due to the black tips of many guard hairs, or a brighter, rusty-reddish color. Anterior part of muzzle, circumorbital region and forehead are ochreous-rusty-reddish. Above each eye, a
101 blackish stripe is present. Margins of lips and lower cheeks are dirty white. Upper part of forehead and occiput are ochreous. Back of ears is pale-rusty; ears are covered internally with dirty whitish hairs. Chin and throat are whitish, with a dirty tint.

Black guard hairs are especially developed on the back, but less so on the sides, and general color here is brighter and clearer. Belly is whitish along the midline, and in the axillary region and groin the color is mixed with a reddish tint. Extremities are ochreous-red, with internal surfaces of lighter color. Tail is gray with an ochreous tint and a strongly defined dark color on dorsal side and at tip. General color intensity and the degree of development of darkening is quite strongly variable individually, and both comparatively dull jackals as well as those with very bright colors are encountered.



Fig. 36. Jackal, *Canis aureus* L. Sketch by A.N. Komarov.

*Russian word is "lobastaya", referring to the more expanded frontal region of the wolf compared to the jackal—Sci. Ed.

Summer fur is more sparse, coarse and short and has same color as that of winter, but brighter with dark tint less developed. Sexual differences in color are absent. Pelage of newborns is very soft and its color varies from light-gray to dark-brown. This pelage remains on the animal for about one month and then the first adult coat starts to grow and is developed by August. It is very similar to that of adults. Geographic variation in color is fairly noticeable.

The skull is similar to that of the wolf in its main features and in general appearance, but is smaller and less massive. The nasal region is lower, and the facial shorter (its length is nearly equal to that of the cranial region), dorsal profile of the facial region is nearly straight and depression in middle of nasal bones is very weak. In the region of the carnassial teeth, the skull is not broadened and its outline, beginning with the line of the zygomatic arches, converges anteriorly in a quite regular wedge (on looking up at the skull from below, a sharp projection in front of the carnassial tooth is not seen). Sagittal and occipital crests are well developed, but weaker than in the wolf. Supraorbital processes are large, but relatively less massive than in the wolf. Between the frontals and between the nasals, along the corresponding sutures, a shallow longitudinal depression is present. On the line of the anterior margins of the nasal bones (at suture between 2 nasal bones) there is a distinct projection (Fig. 15). At the anterior internal borders of the auditory bullae at the basioccipital, the bulla is not bordered by bony ridges.

Canines are large and strong, but relatively thinner than in the wolf, and carnassial teeth are relatively weaker. The cingulum on the outer margin of the first upper cheek teeth is continuous, broad and well defined throughout its whole extent (Fig. 16).

Sexual differences in the skull are only manifested in the generally somewhat smaller dimensions of the female. Age variations correspond, in all principal aspects, with those described in the wolf.

Diploid number of chromosomes—74.

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Male body length 71–85 cm (as a rare exception in the species, may be somewhat more), females average somewhat less.⁴

⁴In regions on the right tributaries of Pyandzh it was shown (Chernyshev, 1958) that body length of males (14) is 68–104 cm, and of females (17) is 71–100 cm. These maximal figures are, apparently, exaggerated. Such figures are not given by any of our authors for either Middle Asiatic or Caucasian animals. Mean body length, drawn from the tables given by the mentioned authors, is 81.5 cm for males and 80.5 cm for females. The maximal specimen, of 75 caught in India, Baluchistan and Iran had a body length of 81 cm (male) and 73.5 cm (female). Six females from Nepal had an average body

Measurements of animals from southern Tadzhikistan (region of the right tributaries of Pyandzh and upper Amu-Dar'ya) are as follows. Adult (sexually mature) males: tail length (14) 22–27 cm, length of hind foot (13) 13.7–19 cm, height of ear (8) 6.7–10 cm. Adult females: tail length (17) 20–27.5 cm, length of hind foot (17) 9.5–12 cm, height of ear (15) 7.1–9.1 cm. Height at shoulder (12) of males and females 44.5–50 cm, height at sacrum 40–48 cm.

Weight of males (15) 6300–13,670 g, of females (16) 7000–11,240 g.

Weight of heart 100–150 g, of liver 185–480 g, total length of intestine 335–454 cm, length of caecum 7.5–12 cm (Chernyshev, 1954).

Measurements of male skulls (14 from Caucasus and from Turkestan; Ognev, 1931; ZMMU*): condylobasal length 147–164 mm, zygomatic width 79–97 mm, breadth of muzzle above canines 27–32 mm, interorbital 22.6–30.2 mm. Skull of females (17) from the right bank of upper Amu-Dar'ya (Chernyshev, 1958): condylobasal length 123.7–159.7 mm, zygomatic width 69.9–92.5 mm, length of upper toothrow 64.5–87.5 mm; interorbital width 19.4–30.1.

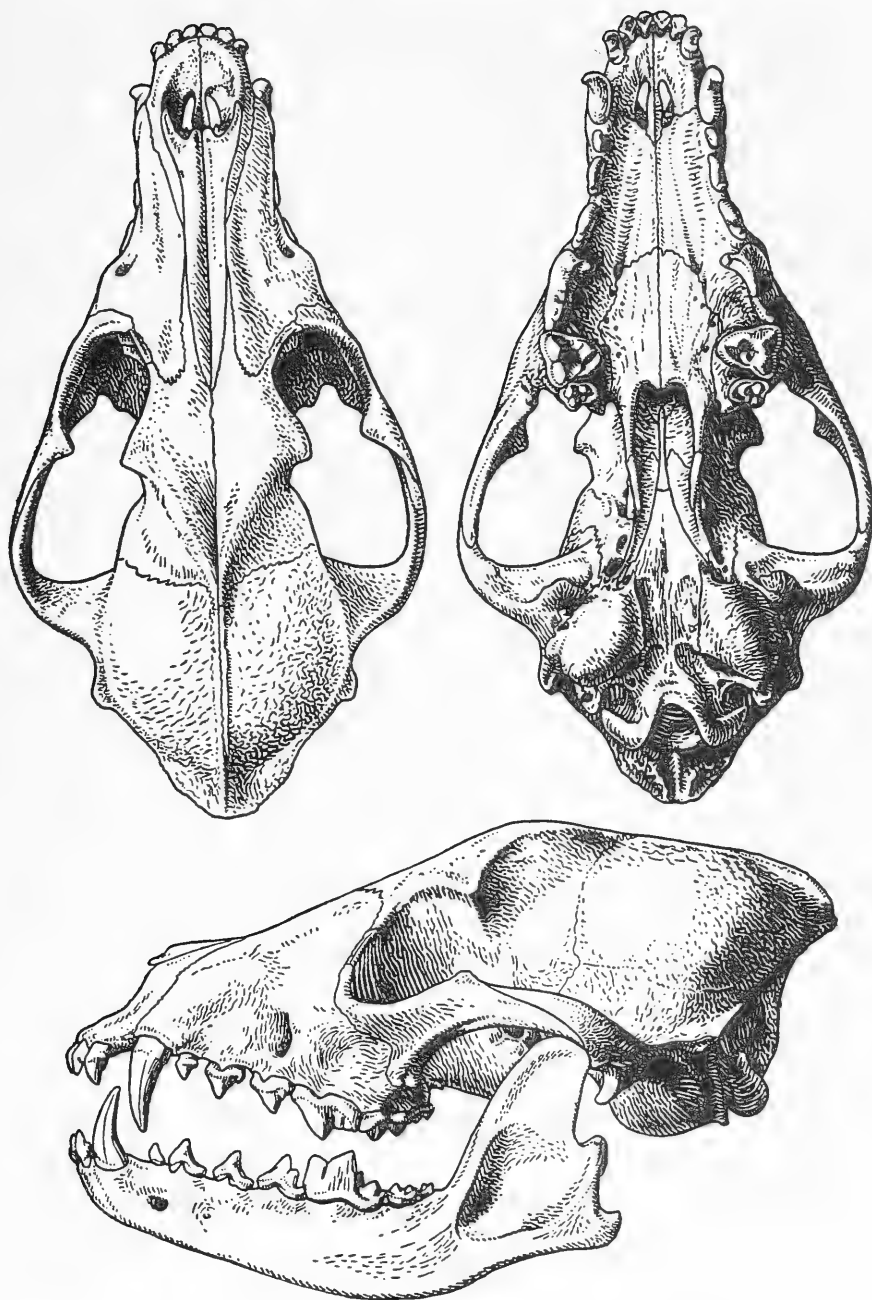
Measurements of jackals within the USSR do not show clear geographic variation. (V.H.)

Systematic Position

The jackal must be considered as a somewhat less specialized form of the genus than the wolf. This is manifested in the relatively short facial portion in the somewhat weaker tooth row, with which, in particular, the above-mentioned "wedge-shaped" skull and its relatively small width in the region of carnassial teeth is connected, and in the less developed crests. This is, apparently, connected with its diet of small prey—birds, rodents, lower vertebrates, insects, other animals and carrion. The jackal

length of 73 cm, 12 females from Palanpur and Sind—69 cm (Pocock, 1941). It is generally considered that Indian animals have a body length of 61–76 cm (Prater, 1947). Maximal Balkan jackals had a body length of 85.5 (male) and 81 cm (female; Atanasov, 1953). Our jackals are, apparently, slightly larger than the Indian ones, but not by much. It is considered, under the circumstances, a mistake, that the skull dimensions given for Tadzhikistan, do not differ from generally known ones. One foreign author (Van den Brink, 1958), who did not refer to the source, gave still more exaggerated dimensions for the European jackal: 85–105 cm, and another (Marches [et al.], 1954) gives a body length of 104 cm for a male and 100 cm for a female from Romania. A weight for jackal of "more than 16 kg" (P. Manteifel; Chernyshev, 1958) is also exaggerated.

*Zoological Museum, Moscow State University.



is a "scavenger" in no lesser degree than it is a predator. This is, apparently, the significance of the somewhat smaller general dimensions of the animal (V.H.).

Geographic Distribution

Southern Asia and Near East, southeastern Europe, northern half of Africa.

Geographic Range in the Soviet Union

This constitutes a considerable part of the species range—its northern border is connected with the southern part of the country—Caucasus, Middle Asia and Moldavia. It consists of several parts within the Soviet Union separated from each other which unite beyond our borders.

104 In the Caucasus, the range of the jackal is connected with the plains and foothills, in places with low and even middle montane belts, and having quite complicated contour. In the western half of the country, the jackal is distributed in a narrow strip along the entire Black Sea coast from Novorossiisk to Batumi. Here, the animals are not usually distributed in mountains higher than 400–500 m above sea level. The range widens somewhat along the Rion Basin and extends somewhat to the east of Kutais'.

In the beginning and middle of the past century, the jackal was, apparently, distributed (perhaps in part as vagrants, however this was not very rare) along the eastern shore of the Azov Sea to the lower Don and even to Taganrog. Old reports about the occurrence of the described species in Crimea are not worthy of attention.

In the eastern half of the Caucasus, beyond the Main Range, the jackal is distributed on the plains and foothills and, as a rule, is not found on mountains higher than 800–900 m above sea level. Only in Zakatal, in autumn, it may climb up to 1000 m searching for fruits, and everywhere in Talysh, to a height of 1700 m (the highest occurrence known in the USSR). In the Trans-Caucasus, the jackal is distributed from Talysh and the Lenkoran lowland southward to the Apsheron peninsula and the foothills of the Great Caucasus on the north. Here, it extends to Zakatal and a little more to the north. In the west, the jackal is distributed along the lowland places of the Iora, Alazan' and Kura basins, to the Tbilisi meridian and a little to the west (Mtskheta). Southward, the foothills of the Little Caucasus constitute the western border of the eastern Trans-Caucasian part of the range.

Along the valleys of various rivers, the jackal penetrates in some places in a minor way into the mountains. Along the Araks valley, the range extends in a narrow strip westward to Oktemberyansk region (44° E. Long., a little east of Erevan). In the Araks, the animal does not ascend higher than 500–850 m above sea level.

From the Apsheron peninsula, the range of jackal extends, in a narrow strip, along the Caspian Sea northward to the mouth of the Terek and Kuma and to the Beryuzyak peninsula. In part of the range northward to Makhachkala, the jackal is distributed along the sea shore, generally not further than 20–30 km from it. Beginning only at Makhachkala, it goes deeper into the country along the foothills and river valleys. To the west of Makhachkala, the jackal is distributed in a narrow strip along the foothill belt to Khasav'yurt and a little westward. It goes west along the Terek to Shelkova (Shelkozavodsk) and Parabochevsk forest and reaches Mozdok, and along the Sunzha, to Groznov. It is not found along the Kuma river upstream from its mouth.

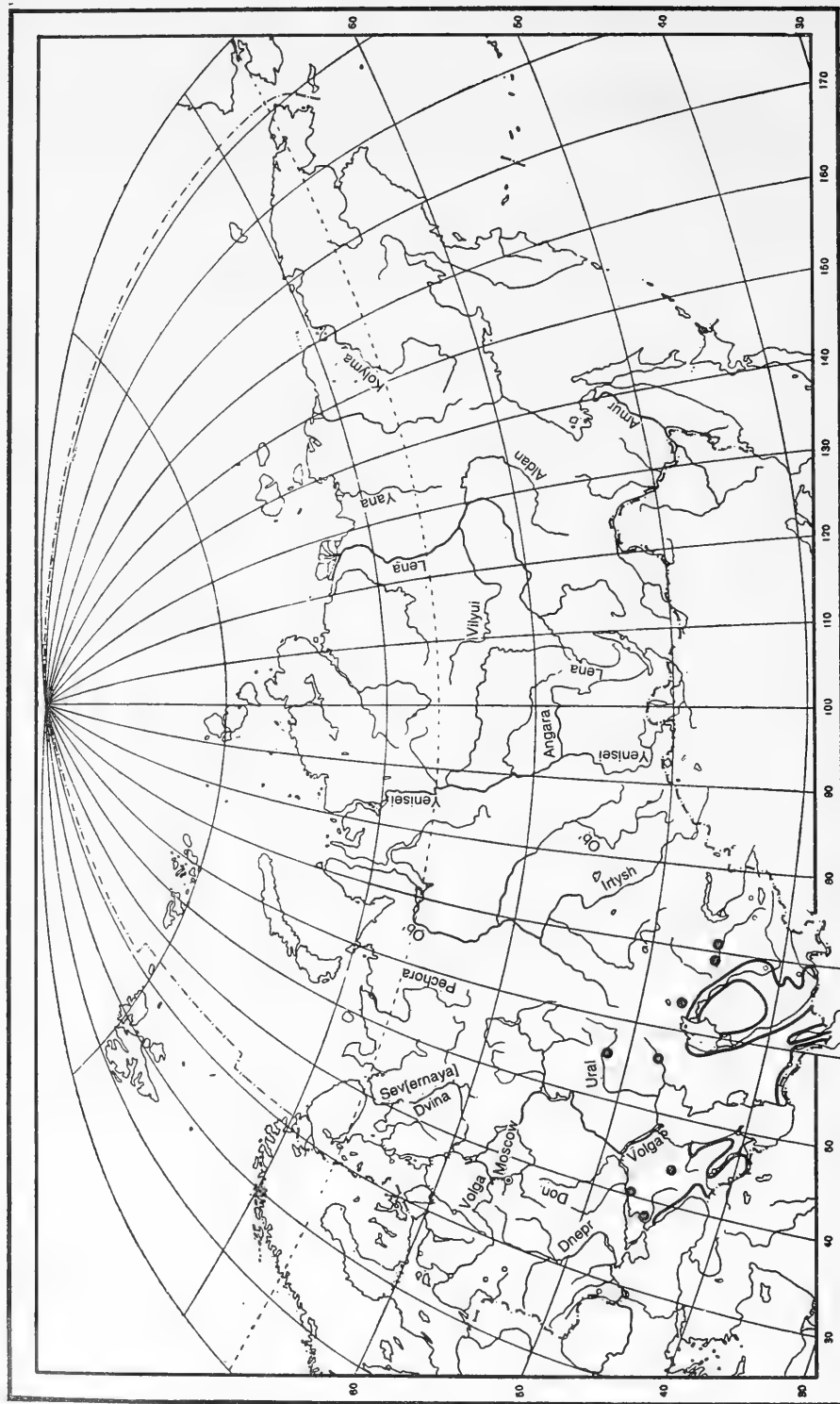
In the past, jackals (apparently, mainly along the Caspian coast), reached the delta of the Volga (30's and 40's of the nineteenth century) and were also found in "Don steppes" and still in the middle of the past century along the Ergeni river. They also inhabited Stavropol' at that time. It is now impossible to decide whether the places of occurrence along the Ergeni and Don were connected with the Pri-Caspian region of occurrence of the species, or with the Pri-Azov region. It is probable that all these were one region.

Of the Caspian Sea islands, the jackal lives only on Sar Island at Lenkoran'. It is absent on other even larger (Chechen') islands as well as on Agrakhansk peninsula (spit).

In the last ten years, to a considerable degree in connection with the drying of the Caspian Sea and the disappearance of reed beds, the range of the jackal in the northern Caucasus has contracted. In particular, it does not reach Kuma.

In the northern Caucasus, chiefly at the beginning of the present century, fairly long intrusions are known—to Gunib in the heart of the mountains of Dagestan, to Stavropol', to Psebai (south of Armavir), to the mouth of the Kuban' river and even into the mouth of the Don. Wanderers in the eastern parts apparently came from the Kizlyar region of occurrence of the animal, and in the west, from the Black Sea coast. Jackal intrusion even to Tambov (Ognev, 1931) is known, probably from the Caucasian region of occurrence of the animal.

106 The distribution areas of the jackal in the western and eastern halves of the Caucasus are, in essence, separated from each other, but



105 Fig. 38. Range of the jackal, *Canis aureus* L. in the USSR. Points beyond the limits of the range refer to several distant intrusions. V.G. Heptner.

in the middle of the Trans-Caucasus they are very near to each other, separated only by the Suramsk range and the adjacent regions—a total of 100 or 100+ km. Animals occur only as intruders and their movements, apparently, reflect some kind of connection that is or was realized between the two described divisions of the range. The present union of the above-mentioned parts of the distribution area applies, however, only farther the south, outside the boundaries of the USSR.⁵

The Middle Asiatic region of jackal occurrence within the Soviet Union is completely isolated from that of the Caucasus. It has quite a complicated form. This is explained by the fact that the jackal, in its distribution here, is associated with river valleys and cultivated lands, resolutely avoids deserts, and does not go high into the mountains. It is, in part, divided into separated sections, isolated from each other. In the west, in Turkmeniya, the jackal is found along the Atrek, from Chikishlyar westward to the mountains. Along the river valleys of the Atrek, Sumbar and Chandyr, it penetrates into the western parts of the Kopet-Dag (at least to Kara-Kala on the Sumbar and Yarty-Kala on the Chandyr), but it does not get into the heart of the Kopet-Dag mountains. Its range envelops the Kopet-Dag from the west (?) and north as a narrow strip along the foothill plains and foothills, and extends to Tedzhen⁶. The jackal occupies the entire Tedzhen valley to its extreme lower reaches and all the valley of the Murgab with its upper tributaries (Kushka, perhaps Egri-Gek). In the desert between the Tedzhen and Murgab, and between the Murgab and Amu-Dar'ya, the jackal is absent. The union of these sections is realized in Iran and Afghanistan.

Along the Amu-Dar'ya, the jackal is distributed from the Chubek (on the river, somewhat east of the mouth of the Kizyl-su, nearly directly south of Kulyab) to the delta which occupies the whole region. In the basin of the upper Amu-Dar'ya, the jackal is distributed along the Kizyl-su and Yakh-su northward, nearly to the latitude of Kulyab or somewhat farther north; along the Vakhsh, it goes up to Kurgan-Tyub; along the Kafirnigan, nearly to Dushanbe or a little to the northeast, to the mouth of the Varzob; along the Surkhan-Dar'ya

⁵The distribution in the Caucasus according to materials of Nordmann, 1840; Kornilov, 1859; V.V. Shch., 1887; Alferaki, 1910; Satunin, 1915; Ognev, 1931; Heptner and Formozov, 1941; Dal', 1954; Heptner, Turova and Tsalkin, 1950; Kirikov, 1959 and the unpublished material of V.G. Heptner.

⁶The distribution of the jackal in this region is poorly delimited. Apparently, the mentioned strip is not continuous. In sand and loess deserts, the jackal is absent. It is also absent in the Great Balkhan and hardly reaches the West Uzboi.

upstream, at least to Regar. In this way, the range includes the entire Gissar valley and the foothills of Gissar range eastward to Ordzhonikidzeabad and almost to Ramit. Between the Surkhan-Dar'ya [river] and Kugitangtau and Baisun[tau] mountains, the range protrudes northward from the Amu-Dar'ya, extending to the city of Chirabad. In all the described sections on the right bank of the Amu-Dar'ya, the jackal does not ascend higher than 1000–1100 m above sea level and the boundary of its distribution envelops, as it were, the higher regions such as Babadag and other massifs lying along watersheds, and forms here a fairly complicated pattern.



107 Fig. 39. Reconstructed species range of the jackal, *Canis aureus* L. V.G. Heptner.

The range of the jackal further occupies the entire area of cultivated land along the Kashka-Dar'ya (Karski, Chakhrizyabs). This region, apparently, is more or less isolated from the previously mentioned Baisuntau mountains. The jackal exists everywhere in the Zeravshan basin (Bukhara and Samarkand oases), penetrating upwards along the river to the mountains, to Pendzhikent, and perhaps somewhat higher. The jackal inhabits the cultivated strip and adjacent places between Samarkand and Tashkent and is widely distributed in Tashkent oasis, eastward to the mountains. Along the Syr-Dar'ya, it penetrates to the western parts of the Fergana valley and to the Farkhandsk reservoir and Kanibadam (for the eastern parts of the valley, almost nothing is known). Downstream along the Syr-Dar'ya, the jackal is normally distributed to the mouth of the Aris. East of the Syr-Dar'ya, at the northern limits of its distribution, it extends to Shimkent, Lenger, Georgievk' and Boroldaisk mountain, and to the sources of Bugun river lying approximately 150 km north of Chimkent.

In Middle Asia, distant intrusions of the jackal are also known and moreover they take place partly in years of severe cattle losses (continuous snow cover)*. In these years, intrusions are more frequent and extend particularly far. Intrusions of jackals may occur in the lower Syr-Dar'ya, reaching Kazalinsk; on the Sary-su river; on the Chu river to its lower reaches; to the northwestern edge of the Betpak-Dala desert and almost reaching even to the city of Karaganda. To the north intrusions are known to the Ustyurt (Kos-Bulak mountain), on the northwestern shore of the Aral Sea (Kintekchi), in the Asmantai-Matai sands at the northern base of the Ustyurt, at Emba. Jackals wandered Turgai and Sary-Kopa and even to Orenburg (see below for details)⁷.

The third region in which the jackal is known in the USSR is Moldavia. Here, the animals are rare, appearing as vagrants, and not coming this far every year, in the southern and southwestern regions. They enter from Romania (Kuznetsov, 1952). The appearance of the vagrant jackals in the Trans-Carpathian region cannot be excluded.

*The Mongolian word *dzhut* refers to persistent continuous snow cover that prevents ungulates from feeding—Sci. Ed.

⁷Range in Middle Asia according to Ognev, 1931; Laptev, 1934; Flerov and Gromov, 1934; Flerov, 1935; Shestoporov, 1936, 1936a, 1936b; Gromov, 1937; Leviev, 1939; Salikhbaev, 1939; Sludskii, 1939; Sultanov, 1939; Kuznetsov, 1948; Bazhanov, 1951; Shukurov, 1951; Afanas'ev et al., 1953; Chernyshev, 1954, 1958; Heptner, 1956 and others and according to the unpublished material of V.G. Heptner.

Geographic Range outside the Soviet Union

The range in Asia includes southwest Siam, Burma, Assam, Bengal, all of India; in the north, it includes Bhutan, Sikkim, Nepal (in Himalaya to a height over 3000 m above sea level), Ceylon, Baluchistan and Afghanistan (except the montane areas of the Hindu Kush), Iran, Asia Minor and the entire Arabian peninsula. In Africa, the range includes Kenya, Ethiopia, Somalia, Sudan, Egypt, Libya, Tunisia, Algeria, Morocco, Rio de Oro [Spanish West Africa, now Western Sahara], and Senegal. In Europe, the jackal is found in Greece, Albania, Yugoslavia and Bulgaria. As a vagrant known in Hungary (in the north to Komitata Khevesh near Tissa northeast of Budapest) and in Romania (very rare, only in the southwestern part of the country at the Danube south of Kraiov)⁸. (V.H.).

Geographic Variation

Throughout a broad area covering the country, with extremely different natural conditions, geographic variation of the jackal is quite well defined, though less than what is accepted. Features of size as well as color vary. In the USSR, there occur two well-differentiated forms.

1—Turkestan jackal, *C. a. aureus* Linnaeus, 1758.

General color is relatively pale with sandy tones predominating. The fur is relatively soft. Dimensions large.

Middle Asia. Outside the USSR—Afghanistan, Iran, Iraq, Arabian peninsula, Baluchistan, northwestern India (Kutch, Sind, Gujarat). That animals inhabiting southwestern Turkmeniya are not completely identical to those living east of the Amu-Dar'ya is not excluded.

2—Caucasian jackal, *C. a. moreotica* Geoffroy, 1835 (syn. *typicus, caucasicus*).

General color is bright and saturated, with strongly pronounced dark blackish tones on the back. Thighs and upper parts of legs, ears and forehead are bright, reddish chestnut. Fur is coarse. Size somewhat less.

Caucasus, Moldavia. Outside the USSR—Southeastern Europe, Asia Minor.

* * *

⁸Calinescu, 1930; Atanasov, 1953. Judging by the catch in Moldavia, one may consider that intrusions occur also in other parts of Romania and take place more frequently than is known.

In territories lying beyond our borders, the following forms are usually accepted: *C. a. syriacus* Hempr. et Ehrenb., 1833 (Syria, Palestine); *C. a. lupaster* Hempr. et Ehrenb., 1833 (Libya, Egypt, Palestine); *C. a. indicus* Hodgs., 1833 (Nepal, Sikkim, Bhutan, Assam, Burma, Siam); *C. a. naria* Wrought., 1916 (south part of India); *C. a. lanka* Wrought., 1916 (Ceylon); *C. a. algiriensis* Wagn., 1841 (Tripoli, Algeria, Tunisia); *C. a. maroccanus* Cabrera, 1921 (Morocco); *C. a. soudanicus* Thos., 1903 (Egypt, Nubian desert, Kordofan, Sudan). Some of these forms are highly doubtful. Sometimes the accepted (Ellerman and Morrison-Scott, 1951) *C. a. cruesemanni* Matschie, 1900, described according to a living specimen by an author of very little reliability, is not taken into account here. The existence of the name *ecsedensis* Kretzoi, 1947 (*hungaricus* Ehlik, *minor* Mojsis.) given to animals from Hungary is also not credited. These are, undoubtedly, vagrant specimen of the Balkan *moreoticus*; jackals do not live permanently in Hungary.

The statements that there are 20 species of jackals in the Old World, not including the black-backed (Ognev, 1931), is completely unsubstantiated. The true jackals, together with the black-backed, are only 3 species (*aureus*, *adustus*, *mesomelas*). The previous conception was based on binary designation of races, the unnecessary division of species and subspecies and upon unreviewed synonymy. (V.H.)

Biology

Population. Along the Caucasian coast of the Black Sea, at Novorossiisk, the jackal is rare; to the south, it is common, while in Georgia it is abundant. At the mouth of Terek, it is rare; southward, its number increases, reaching a maximum in southern Azerbaidzhan. In Dagestan, from 1936 to 1941, an average of 580 jackal furs were prepared yearly. The jackal is abundant in the Kolkhid, Zakatalo-Ismailinsk, Kurinsk, Lenkoran and other lowlands in Georgia and Azerbaidzhan. In Armenia and Nakhichevan Autonomous SSR, they are encountered in small numbers. In the Trans-Caucasus, in the 30's of the present century, up to 17 thousand jackals were caught yearly. In the Trans-Caucasus, jackals are most common in Azerbaidzhan. From 1931 to 1940 an average of 9400 animals was caught here yearly, in Georgia—2300, in Armenia—some hundreds (Vereshchagin, 1947).

In Turkmeniya, it is abundant in the valleys of rivers and rare in the foothills and low mountains, from whence, from time to time, it penetrates in small numbers to the very edge of the desert. In higher

areas deep within the Kopet-Dag, it is absent or rare (V.G. Heptner). On the lower Atrek, it is not numerous and comparatively few are captured (106 in 1941; Samorodov, 1953). It is rare in West Uzboi. In the valleys of the Tedzhen, Murgab, and Amu-Dar'ya rivers, and in the oasis irrigated by them, it is abundant; and is more rarely met with along the Sumbar and Kushka. In the mountains of southern Turkmeniya, it is encountered regularly. It is known in Karabil', the mountain between the Kushka and Murgab rivers, and on the Gyaz'-Gyadyk (upper Tedzhen), but in small numbers (V.G. Heptner). From 1948 to 1958, from 1400 to 5400 jackals were caught annually in Turkmeniya (Sapozhenkov, 1960).

In Tadzhikistan, jackals are abundant in the valleys of the Pyandzh, Vakhsh, and Amu-Dar'ya rivers and their tributaries—the Kafirnigan, Kyzyl-su, Surkhan-Dar'ya and in the adjacent cultivated lands. In the offshoots and foothills of the mountains they are rare. It is especially numerous in the Pyandzh tugais* from Faizabad-Kala to the mouth of the Vakhsh and along the entire Vakhsh valley where, however, they avoid sandy deserts. In the settlement of Tigrov Balka in the Pyandzh valley, in 1946–47, on an area of 600 hectares, about 133–161 jackals were counted, i.e. up to 0.02 individual per hectare. In the mountains of the Vakhsh–Kafirnigan interfluvium, it is encountered only during migrations. To the west of the Kafirnigan, and to the north of the Amu-Dar'ya tugais, it is very rare in the foothills of Koikutau and Tuyuntau, inhabiting the whole of the cultivated strip of the Gissar valley, and it is also not rare in the foothills of Gissar range (Flerov, 1935; Chernyshev, 1954, 1958). It is common in the valleys of the upper reaches of the Syr-Dar'ya and Zeravshan rivers (Chernyshev, 1954). From 1951 to 1958 from 530 to 1400 jackals were caught in Tadzhikistan.

In Uzbekistan, the jackal is numerous in the valleys of rivers Surkhan-Dar'ya, Kashka-Dar'ya, Zeravshan, Syr-Dar'ya, in the lower Amu-Dar'ya and in Khorezm and Bukhara oases; it is rare in foothills and also in the Fergana valley in the floodplains of the Naryn and Syr-Dar'ya rivers. In Fergana, it is captured occasionally (Malenkov, 1958). Only in the lower Amu-Dar'ya, in the territory of Karakalpak Autonomous SSR, are about 1000 jackal furs prepared yearly (Kostin, 1956). In the Amu-Dar'ya delta about 200 jackals were estimated in 1948 on six tugai woodlots (Salikhbaev, 1950). From 1950 to 1958, from 3300 to 6200 individuals were prepared annually in Uzbekistan.

*The Russian *tugai* refers to a distinctive riparian shrubland found along rivers of Middle Asia—Sci. Ed.

It is rare in the Syr-Dar'ya valley in its middle course north of Kzyl-Orda, but in some years, it is very common from its confluence with the Arys' and farther south, and also in the spurs and foothills of the Talask Alatau in the territory of Chimkent'sk district.

Habitat. In the Caucasus and Trans-Caucasus, the jackal is a lowland dweller, and as a rule does not ascend into the mountains higher than 600 m above sea level. Only in a few places (Borzhomi), it is found at a height of 900–1050 m (Dinnik, 1914), and in Armenia at present climbs to heights of 840 m (Dal', 1954). It inhabits the coasts of the Black and Caspian seas and the level valleys of rivers everywhere where there is dense forest, thickets of prickly bushes and extensive reed floodlands rich in game and small rodents. Where dense shrubs are absent, jackals are absent. Preferred habitats are impassable thickets of bushes, consisting of various spiny and climbing plants such as blackberry, Jerusalem thorn (*Paliurus australis*), *Smilax excelsa*, *Clematis* sp. and others. In these thickets, the yearly falling leaves and the dry branches form, at some height from the ground, a unique flooring that divides the thicket into two levels: in the lower, the inhabitants of these thickets move freely—jackals, jungle cats, badgers, wild boars, pheasants and others feeling themselves here to be in comparative safety (Satunin, 1915). Such habitats serve as shelters for jackals in southern Dagestan, on the lower Samur. They are nearly inaccessible to humans, but the animals freely move there along "tunnels" made by wild boars (Heptner and Formozov, 1941).

The jackal hunts along rivers and canals, on the sea shore and around lakes, beating down, together with other animals, the trail system. In dry years, when lakes and swamps dry out strongly, jackals concentrate around them, hunting waterfowl, nutria and small rodents. In severe winters, when water bodies are covered with ice, the carnivores gather around them, cross over to the island and settle in the reedbeds away from the shore and through the course of the entire period of frost, do not leave the water bodies. In spring, summer and autumn, 70 jackals and 60 jungle cats were caught in a small section of the Inkitsk swamps (Georgia) (M. Pavlov, 1953). Jackals live very close to settlements. One time a jackal lived in the center of Lenkoran village under a forester's house.

In Middle Asia and Kazakhstan, the jackal is also a lowland dweller. Here, the preferred habitats are tugai thickets and reed floodlands in the floodplains of rivers, bushes and reeds along the canals and *aryks*,* and

*The Russian *aryk* is a Turkic loan word for irrigation ditch—Sci. Ed.



Fig. 40. Habitat of jackal. Outer margin of tugai of tamarisk and turanga, in the Murgab valley at Imam-baba, Turkmeniya, 22 May 1962. Photograph by A.A. Sludskii.

also thickets on abandoned irrigated lands. They prefer wild olive-turanga and tall grass-herb tugais. Here, trees are densely interwoven with vines and surrounded with sturdy thickets of reeds or plume grass
 111 [*Erianthus*]. Places where jackals live usually abound in waterfowl, pheasants, tolai hares, small rodents, frogs and fish. Here it finds good cover and abundant prey.

In the Gissar and Fergana valleys, jackals do not find hiding places in the arable fields in the valley, and live in adjacent low hillocks [called] *adyr*. In the *adyrs* it shelters in dry channels, loess caves and niches, occupying abandoned holes of foxes and porcupines, or digging its own holes. In Turkmeniya, if there are not good thickets along the river, as for example on the Kushka, the jackal also makes a hole found in the neighboring hillocks (Heptner, 1956).

The jackal willingly settles in oases, where it confines itself to thickets along irrigation ditches and reservoirs, in gardens, graveyards, ruins, etc. In Bairam-Ali, on the lower Murgab, jackals colonized and dug holes in planted groves of white acacia in a very populous place (V.G. Heptner). In Middle Asia, the jackal is, to a considerable degree,



Fig. 41. Biotope of jackal—tugai on the Murgab at Sultan-bent. Turkmeniya, 10 June 1962. Here also the spotted [steppe] cat and wild boar are found. Photograph by A.A. Sludskii.

a synanthropic animal. It is especially abundant in very old oases, such as Tedzhen, Pendin or Merv on the Murgab, Bukhara on the Zeravshan, and Khorezma on the Amu-Dar'ya. In connection with irrigation and utilization of deserts and the establishment of new oases in the 30's—50's of the present century, rapid colonization of jackals was observed in the new regions lying in the Vakhsh—Pyandzh interfluve, in the Golodnaya steppe of Uzbekistan and in other places. A further increase in the number and dispersion of jackal may be expected.

The jackal avoids waterless deserts, being encountered there only at their very edge. As a rule, it does not live in the Karakum and Kyzylkum, but is met with in significant quantities along the borders of the sandy deserts, adjacent to the Murgab and Amu-Dar'ya oases (Salikhbaev, 1950; Stal'makova, 1955), where it comes out from the tugais and thickets in order to hunt gerbils. In Repetek, situated only 70 km away from the Amu-Dar'ya, jackals were not observed (Stal'makov, 1955). However, in the fall of 1957 and 1958, they appeared here (Sapozhenkov, 1960). They appear in the Asmantai sands

- in the Ustyurt, migrating from the delta of the Amu-Dar'ya and from the shore of the Aral Sea. In foothills and mountains they are confined to tugai shrubs along ravines, and in bushes along rivers and gullies.
- 112 In the Himalayas, it ascends somewhat higher than 1000 m above sea level.

The presence of jackals in one or another region and their choice of habitats are determined by the abundance and availability of prey, the presence of water and dense shrubs which serve as shelters both for the jackals themselves and for the animals which they hunt. It is especially abundant there where water bodies incur no prolonged freezing period and where it is possible for waterfowl to overwinter.

Jackal can withstand low temperatures down to -25° [C] and even -35° , but it is not adapted to live in very snowy lands. In the Trans-Caucasus, in severe winter with much snow (1949–1950), jackals could travel only on roads and paths made by humans and large animals (Vereshchagin, 1951).



Fig. 42. Habitat of jackal on the Murgab. Tugai of turanga and tamarisk at Sultan-bent, Turkmeniya. 10 June 1962. Photograph by A.A. Sludskii.

Food. The jackal is a predator-scavenger but, at the same time, it readily eats all available carrion and refuse, and feeds on large quantities of plant food, being, in some seasons, omnivorous.

In the Caucasus and Trans-Caucasus, it mainly hunts hares and mouse-like rodents, as well as pheasants, francolines [*F. francolinus*] (when they were numerous), ducks, coots [*Fulica atra*], moorhens [*Gallinula chloropus*] and passerines. Birds suffer greatly from it at the time of autumn migration and when wintering. It frequently attacks domestic birds, including turkeys, more rarely lambs, sheep and goats and one even attacked a newborn domestic buffalo calf (Dinnik, 1914; Satunin, 1915). They willingly eat lizards, snakes, frogs, fish, molluscs, insects, floating dead fish and various [kinds of] carrion. It frequently feeds on fruits such as pears, hawthorn, dogwood, and "cones" of *Mespilus germanicus*. It chooses sweet sorts and avoids sour. In gardens, it destroys many grapes, eating watermelons, muskmelons and nuts (Dzhanashvili, 1947). In 26 feces samples collected in summer, 1950, in the Ismaillinsk region (Azerbaijan), mammals were found in 90.0% of the total sample, birds—27.0%, reptiles—23.1%, 113 amphibians—15.4%, insects—19.2%, plants—26.2% and carrion—7.7% (Rukovskii, 1953). In 12 feces samples from Lake Shil'yan (Azerbaijan) mouse-like rodents were found in 3.3% of the samples, water vole [*Arvicola*]—25.0%, European hare [*Lepus europaeus*]—25.0%, carrion (wild boar, dog)—16.7%, coot—8.3%, discarded fish—8.3%, insects (locust)—40.1% and squash seeds—16.7% (Pavlov, 1953).

In severe winters, when water bodies freeze, jackals cause great losses among nutria, coots and ducks. In the winter of 1948/49 in Trans-Caucasus, nutria occupied first place in the jackal diet (Table 4).

In such winters, mouse-like rodents, small birds and other foods play a small role in the jackal ration. In winter, in the presence of abundant prey the jackal kills more animals than it can eat, and caches excess food. Jackals feed in a similar manner in Middle Asia and Kazakhstan (Table 5). Rodents occupy the principal place and then birds (20.0%).

Some role is also played by fish and arthropods, of which locusts and darkling beetles are more frequently eaten (Chernyshov, 1954). In some instances the stomachs of jackals are entirely filled with locusts (Flerov, 1935).

In the nutritional ration of the jackal, wild and cultivated plants are of serious significance. Thus, the stomach contents of 23 jackals caught

Table 4. Winter foods of jackal in Trans-Caucasus in the severe winter of 1948/49 (in % of the total number of samples investigated) (Pavlov, 1953)

Food designation	Gagrsk region Abkhazsk ASSR	Kurdamirsk region Azerbaijdzhan SSR	
	Before freezing	During freezing period	
	30 samples	104 samples	17 samples
Nutria	26.6	89.4	47.0
Water vole	3.3	0.9	11.6
Brown rat [<i>Rattus norvegicus</i>]	13.3	2.8	5.9
Voles	—	—	5.9
Asia Minor gerbil [<i>Meriones tristrami</i>]	—	—	5.9
Small mouse-like rodents	26.6	18.2	—
Birds	36.6	76.9	64.7
Including:			
coot	—	—	29.3
mallard	—	—	23.5
grebe	—	—	5.9
passerines	—	—	5.9
domestic fowl	10.0	—	—
Fish	6.6	—	—
Insects (beetles)	—	1.9	5.9
Carrion of domestic animals	20.0	—	—

in October–January in tugais on the Vakhsh consisted completely, or in large part, of the fruit stones of wild stony olive (*Elaeagnus angustifolia*) (Chernyshev, 1948). In spring, jackals dig out and eat plant bulbs (Flerov, 1935; Chernyshev, 1954), and later, roots of wild sugar cane (Table 6).

Jackals living near the edge of the Karakum venture out into sandy areas to hunt, where they catch gerbils, lizards and snakes. In the period of drying of canals and irrigation ditches, they feed on fish and frogs, and hunt muskrats. In tugais and gardens, jackals eat fruits of wild olive (*dzhida*)*, mulberry and dried apricots, as well as watermelons, muskmelons, tomatoes and grapes, to which they cause appreciable harm.

In the lower Amu-Dar'ya, in the stomachs and feces of jackals, were found remains of tolai hare, complex-toothed rat [*Nesokia indica*],

**Dzhida* is a local name for wild (stony) olive—Sci. Ed.

114 **Table 5. List of jackal foods in southwestern Tadjikistan based on analysis of gastro-intestinal tract samples (60 specimens) and feces (175 specimens) (Chernyshev, 1958)**

Type of food	% of 235 samples	Type of food	% of 235 samples
Animal food	78.8	<i>Reptiles and amphibians</i>	2.8
<i>Mammals</i>	36.8	Reptiles unidentified	0.8
Mammals, unidentified	2.0	Lake frog	2.0
Carnivores	0.8	<i>Fish</i>	6.8
Badger	0.4	Fish, unidentified	2.0
Marbled polecat	0.4	Gambusia	3.6
[<i>Vormela peregusna</i>]		Common carp	1.2
Rodents	31.2	<i>Arthropods</i>	14.4
Rodents, unidentified	6.0	Insects (majority are	
Tolai hare [<i>Lepus tolai</i>]	11.2	beetles, and others)	9.6
Field rat*	3.2	Plant food	32.6
Turkestan rat	1.6	Melon culture (musk-	
[<i>Rattus turkestanicus</i>]		melon, watermelon)	6.4
Red-tailed gerbil	2.4	Wild olive fruits	14.4
[<i>Meriones erythraurus</i>]		Wild cane sugar	4.0
House mouse [<i>Mus musculus</i>]	6.4	(root, stems)	
Mole-vole [<i>Ellobius</i> sp.]	0.4	Bulbiferous plants	4.4
<i>Birds</i>	20.0	Nightshade fruit	1.6
Birds, unidentified	2.8	Wolfberry fruit	1.2
Pheasant	10.8	Wheat	0.8
Duck	2.4	<i>Carrion</i>	10.4
Coot	0.8		
Passerines, unidentified	3.2		

*Species not clear—Sci. Ed.

gerbils, pheasant and other birds, insects (locust and beetles) and rarely plants (Salikhbaev, 1950). Where there are muskrats and nutrias, the jackal destroys a great number of these rodents (Pokrovskii, 1953; Kostin, 1956).

- 115 They visit the sea shore where they pick up the dead fish, wounded waterfowl, molluscs, and feed on parts of marine animals discarded by processors. They also feed near slaughterhouses, dumps, and cattle burial places. In southern Dagestan in the 20's, jackals regularly fed near the railway lines, picking up food remains thrown out from passing trains by passengers. They were so accustomed to finding edibles, wrapped in paper, that hunters placed poisonous baits along the railway lines, wrapping it in newspaper (Heptner and Formozov, 1941).

114 **Table 6. Seasonal variation in the list of principal foods of the jackal in southwestern Tadzhikistan (Chernyshev, 1958)**

Name of food	Season of year			
	Winter XII, I, II	Spring III–V	Summer VI–VIII	Autumn IX–XI*
Rodents	3 ¹	4	3	3
Birds	3	4	4	3
Reptiles and amphibians	1	2	3	2
Fish	1	2	3	3
Arthropods				
(majority are insects)	1	3	4	3
Wild plants	3	3	3	4
Cultivated plants	3	3	3	4
Carrion, refuse	3	3	3	3

*Designates months of the year—Sci. Ed.

¹Frequency of occurrence of food: very frequent—4; frequent—3; rare—2; very rare—1.

115 In summer the jackal, apparently, needs to drink regularly, since at that time they always stay near water and are not found in waterless deserts. In southeastern Turkmeniya, when considerable sections of the Kushka [river] dry up, jackals, together with wolves and foxes, dig holes in the bottom of the dry channel and drink the ground water collected in them (Yu.K. Gorelov). Eating of watermelons, muskmelons and grapes is also linked with the slaking of thirst.

Home range. In southwest Tadzhikistan, daily movements of jackals sometimes comprise 8–12 km, i.e. the home range of one family in tugai has a radius of up to 12 km. In Tigrovaya Balka Preserve, in an area of 6000 hectares, from 10 to 23 jackal families were counted in different years, i.e., one family occupies an average of from 260 to 600 hectares (Chernyshev, 1954). In Georgia, at Lake Inkit, in the severe winter of 1948/49, seven families of this carnivore occupied an area of 3 × 3 km (M. Pavlov, 1953). The average area for one family there was 130 hectares.

In case of food shortages in some winters, and also after large fires in tugais and reeds, jackals in search of prey were obliged to undertake movements of 40–50 km, regularly appearing in cultivated lands and villages.**

**In Russian original, *kishlak*, a Turkic word for village—Sci. Ed.

Burrows and shelters. In the Caucasus and Trans-Caucasus, the female usually gives birth in a burrow it has dug together with the male, or she occupies the abandoned dwellings of fox and badger. The burrow is dug some days before delivery, and the female and male take turns digging. It is located in thick shrubs, on the slope of a ledge or gulley, or on a flat surface. The burrow is simple in structure, since it possesses one opening which runs to a depth at a small angle. The length of the burrow is about 2 m, while the nest chamber is located at a depth of 1.0–1.4 m. In Dagestan and Azerbaidzhan, jackal litters also were repeatedly found in the hollows of large fallen trees (Satunin, 1915; Dzhanashvili, 1947). In Azerbaidzhan, lairs with pups were found under the roots of trees and under large stones on river banks (Dzhanashvili, 1947).

The litter remains in the burrow for 2–2.5 months after which the female leaves the lair with the young and begins to lead a roving way of life. Regardless of the time of reproduction, the lair is built in dense thickets of spiny bushes (blackberry, Jerusalem, or Christ thorn) or reeds, and rarely in caves, crevices in rocks, hollows, old burrows, water channels and other secluded places.

In Middle Asia, jackals construct lairs in the dense thickets of tugais, and burrows are not dug (Chernyshev, 1954), but they have been described for the Vakhsh tugais (Flerov, 1935). These burrows usually have short, straight passages, dug under the roots of turanga or wild olive, or directly in dense thickets of tamarisk and *Nitraria* sp. One of these burrows, with a length of three meters or more, went obliquely downwards for some distance and widened into the lair itself. In front of the entrance there was a quite large heap of earth which was greatly trampled down in the middle. At a distance of 140–200 m two other holes, similar to the first one, were found. From all the holes, well-packed paths extended through the tugai, which led to a common network of trails. Surrounding the holes were many feces, partially covered with earth.

In the tugais and cultivated lands of Tadzhikistan, jackals construct lairs in the turf of a gigantic grass—plume grass [*Erianthus*], less frequently in *Nitraria* sp., shrubs and in openings in reeds. There, where vegetation may have been destroyed, jackals live in holes. The female, male and young live in one lair (Chernyshev, 1954).

Daily activity and behavior. The jackal basically follows a crepuscular and nocturnal way of life, leaving its diurnal shelter before sunset and returns with the light or even later in the morning. They also often hunt by day. One may judge whether it is leaving to hunt by the

character of its howl. When one animal begins to howl, the others soon answer. Howling is, apparently, also connected in part with the weather. Cases have been noted, when, in case of change in weather, jackals break out in a prolonged and continuous howl. Jackals accompanied with howls the ringing of church bells; the young start to howl when they hear the sound of a siren, or whistle of steamship or train engine. They usually howl in the evening and at dawn, but sometimes during the day, even at midday.

The jackal is a daring and brave animal, and in places where it is not pursued, less cautious and not afraid of people. It is easily caught in traps or envenomed with poisoned bait. Many instances are known, when, within sight of people, it attacked a domestic fowl, and regardless of the shouts and pursuit, takes it off. From field camps and from houses it drags off various objects, which it thinks to be edible, such as leather, boots, rags, venturing to steal them just a few steps from sleeping people.

Jackals usually hunt singly, and less frequently in pairs and in [a group of] 3–4 and only rarely do they form small packs. In the Trans-Caucasus, at the end of summer and in autumn, packs of 8–12 jackals were observed including, apparently, two or more families (Dzhanashvili, 1947). When embarking on a hunt, the jackal jogs along at a trot and frequently stops to sniff and listen. On spotting prey, it stealthily conceals itself, and quickly approaching, pounces and quickly makes a kill. When hunting in pairs or packs, they run in parallel, overtaking the prey together. For example, when hunting nutria or muskrats, they run along both banks of narrow streams or channels, driving the frightened prey from one to another. When lying in wait for its prey, it conceals itself near a path or waterhole. In times of drought, they concentrate near the drying lakes and channels and catch animals and birds on the shore or in shallow water; they also catch fish there. During freeze-up, they hunt waterfowl, nutria and muskrats coming out on the edge of the ice or bank. They attack sleeping flocks of birds (ducks, little bustards [*T. tetra*]) and especially many of them are destroyed in severe winters when they are exhausted from starvation. In autumn, when the canals and irrigation ditches are prepared for cleaning and are dry, jackals together with foxes, jungle cats, badgers, crows, and magpies successfully hunt fish and frogs that have collected in the remaining pools of water, as well as muskrats forced to walk over significant section of dry land. When water bodies freeze, in trying to catch muskrats, they destroy their houses.

The jackals live in pairs, but are also found either singly, or in pairs and families of 4–5 individuals.

Jackals, when taken young, quickly become tamed, following their owner everywhere, and running to his call. They behave as an affectionate dog would. Even adult animals can be tamed. In some places the dogs do not disturb jackals and both animals could be observed together on one garbage heap.

Seasonal migrations and transgressions. Regular seasonal migrations are not characteristic of jackals. They usually wander only in various directions searching for places with food in which they concentrate. Thus, in autumn they gather on the shore, where they pick up bird remains. On sea coasts they are attracted by the carcasses of dolphins or seals thrown out by processors. During fall, the number of jackals in the tugai grows due to the arrival of animals from neighboring cultivated lands. In winter, they wander into human settlements or intrude deep into the desert. During such wanderings, they cross 50–100 kilometers or even more.

117 While not truly regular migration, at the same time jackals often settle at great distances from their usual range, and appear in regions in which they were only a long time ago, or where they are completely unknown (see above). In 1920–1922, when many cattle died of starvation, jackals appeared in considerable quantity in western Kazakhstan, especially in the valley of Ural river; in the north they reached nearly to Orenburg (Sludskii, 1939). The jackal may appear around Orenburg from the delta of the Amu-Dar'ya, passing along the shore of the Aral Sea, through Ustyurt to the Emba and Ural; this way constitutes, in a straight line, about 1000 km.

In the 30's of the present century, the jackal was rare in the middle course of Syr-Dar'ya (Aris' region), but in 1942–1945, it became common there, reached eastward to Chimkent, appeared in the Boroldisk mountains in the upper Bugun 150 km north of Chimkent (Sludskii, 1953). It remained in the latter region until the 50's.

In the winter of 1948–1949, in Kustanaisk district, after an extended continuous snow cover and massive death of cattle on winter pastures, jackals appeared in the summer of 1949, in Dzhangil'dinsk and Amangel'dinsk regions of this district, on the Turgai river and at Lake Sarykopa, and became common. Through 1952, their skins were received in trade. The appearance of jackals in 1949 in the Turgais steppes was accompanied by a massive inflight to this area of brown [*Gyps fulvus*] and black [*Aegypius monachus*] vultures which were

also attracted by the abundance of carrion. On the Turgai river, jackals could pass from the delta of the Amu-Dar'ya along the western shore of the Aral Sea and the Bolshoi Barsuki sands, or also from the Syr-Dar'ya, below Aris', across the lower course of this river and the Priaral'sk Karakum sands. In the first event they might have gone about 1050 km, and in the second—about 1125 km.

In the severe winter of 1950/51 in southern Kazakhstan, jackals appeared at the northwestern edge of the Betpak-Dala desert, in the Dzhetikonur sands, having penetrated there from the Syr-Dar'ya upwards along the Sary-su river, and they remained there in limited numbers until 1954; several animals, in that winter, succeeded in reaching even the upper Sharubai-Nury river 40–50 km southwest of Karaganda. The route thence from the Syr-Dar'ya is about 800 km. In the lower Chu river, the jackal was encountered at the end of the past century, then disappeared and again appeared in 1917. Later, individual animals were caught there in 1927, 1936 and 1948.

In October 1924, a female of a pair was caught 60 km from Tambov (Ognev, 1931). In order to reach Tambov from the lower Terek along the Caspian Sea coast and upwards along the Volga and its tributaries, jackals must have gone about 900 km. The appearance of carnivores in new regions usually coincides with the mass death of ungulates from starvation. It is not clear how jackals and vultures find separate regions where there is much carrion.

In Bulgaria, jackals also sometimes migrate to the north and northwest, appearing near Sofia, at the city of Kotel in Asenovgradsk region, at the city of Dimitrova, and also intruding into Romania, Yugoslavia and Hungary (Atanasov, 1953). In the winter of 1952/53 they appeared in Slovenia, following, apparently, the herded sheep. Prior to this winter, jackals in Yugoslavia were only found in Dalmatia and Macedonia (Berlikh, 1955).

Reproduction. Jackals live in pairs, united apparently, for life, until one of the partners dies. The male helps in digging the burrow and raising the young. In southwestern Tadzhikistan, out of 82 jackals, 39 were males and 43, females (Chernyshev, 1958).

In the Trans-Caucasus, estrus begins in the first half of February, and in warm winters, at the end of January. The mating period continues for 26–28 days (Dinnik, 1914; Satunin, 1915; Dzhanchashvili, 1947). In Tadzhikistan and Uzbekistan, the rut manifested itself at the same time also, and extended to the first days of March (Chernyshev, 1954; Kashkarov, 1931; Salikhbaev, 1950). In Bulgaria, it extends from the middle of January to mid-February (Atanasov, 1953).

118 Gametes in adult males and females do not mature at the same time. Active spermatogenesis in males appears 10–12 days earlier than estrus in females. During the mating period, testes weight increases three times.* In Tadzhikistan, average weight of testes in January was 6.1 g, in February—13.3, in March—13.0, in April—7.7 and in August—4.4. In a male, caught on 6 March 1948, with noticeable degradation of the testes, sperms were still detected. Ovaries increase insignificantly in the estrus period (from 0.7 g in January to 0.8–0.9 g in February–March) (Chernyshev, 1954). Estrus continues 3–4 days. If the female is not mounted during this period, her receptive condition will be interrupted for 6–8 days, after which estrus returns and again continues 3–4 days. If the female does not become pregnant by that time, estrus will not recommence until the next year. Mating can be observed at any time during the diurnal cycle and is accompanied by an attachment [mating tie] which lasts for 20–45 minutes (Dzhanashvili, 1947).

Jackals howl particularly often during the mating period. The female coming into heat for the first time is pursued by several males, and quarrels develop among them. The duration of pregnancy is 60–63 days (Bogdanov, 1873, Pocock, 1941, Brink, 1957); according to observations at Tbilisi zoo—62–63 days (Dzhanashvili, 1947). In Tadzhikistan a considerable number of barren females (5 out of 15) was noticed in different years (1948, 1950). In all of these barren females, helminths were found in great quantities (Chernyshev, 1954).

In the Trans-Caucasus, birth of the young usually takes place from the end of March to the last days of April. The earliest parturition was noted on 28 March 1937 and the latest, on 25 April 1931 (Dzhanashvili, 1947), but sometimes females deliver in the first half of May (Satunin, 1915). In Tadzhikistan, Uzbekistan and Bulgaria parturition occurs in April and the beginning of May. Only once, a female gave birth to 8 pups on June 11th (Chernyshev, 1958; Atanasov, 1953). Only one litter per year is produced.

In the Trans-Caucasus, the number of young in the litter ranges from 3 to 8 (Dinnik, 1914; Satunin, 1915; Markov, 1934; Dzhanashvili, 1947). Satunin (1915) dug out several burrows, in one finding 5 pups, and in the remainder, 4. According to observations in nature and in zoos, the litter usually contains 5 pups, rarely 3–4 or 6–8. In Tadzhikistan, there are 3–7 (average 4.8 pups; Chernyshev, 1958). In

*The weights given in the next sentence suggest that this should read “two times”—Sci. Ed.

Uzbekistan, there are 2–8 pups in a litter (Kashkarov, 1931; Salikhbaev, 1939, 1950). In the majority of regions in Bulgaria, there are 4–7 pups, but in Michurinsk region, only 3–5 (Atanasov, 1953). In India, a litter contains an average of 4 pups (Blanford, 1888).

The female nurses the young for 50–70 days (Caucasus; Dzhanashvili, 1947), in Tadzhikistan up to 90 days. The lactation period in some females ends in the middle of July and in others, in the first days of August (Chernyshev, 1958). The young begin to eat meat starting at the age of 15–20 days. Only in rare instances does the mother feed the pups regurgitated food. At the end of the lactation period, the female drives the young away from her by growling and biting. The latest-born remain with the female until the first half of autumn, after which they leave her and start leading an independent life, either singly or in groups of 2–4 individuals.

Sexual maturity, based on observations in the Tbilisi zoo, takes place in females at an age of 10–11 months, but in males at the age of 21–22 months. In males 10–11 months old, the testes are undeveloped and contain no sperm (Dzhanashvili, 1947). In Tadzhikistan, males are said to become sexually mature at the age of 10–11 months (Chernyshev), a statement which is not true. Duration of life is 12–14 years (Brink, 1957).

Growth, development, and molt. Pups are born with a pelage of soft fur, the color of which varies from light-gray to dark brown. At the age of one month, the juvenile pelage is replaced. At first, guard hairs grow on the head, back and rump, then on the anterior and posterior
119 limbs and, finally, on the tail. Fur color of the young changes, becoming reddish with black speckles. Young caught by the end of August and the beginning of September hardly differ from adults in fur color. By October and November, the young already have full winter fur (Chernyshev, 1958).

Young are born with closed eyelids. In the Tbilisi zoo, in 39 pups (78%) the eyelids opened on the 9th and in the remainder—on the 10th–17th day. Eye-opening is delayed in weak and sick pups (Dzhanashvili, 1947). In Tadzhikistan, based on observations of 9 pups, eyelids opened on the 8th–11th day (Chernyshev, 1958). Ears in healthy pups open on the 10th–13th day and become erected only on the 25th–30th day.

The last [3rd] and middle [2nd] deciduous incisors in the upper jaw first erupt on the 11th–14th day. The inner [1st] deciduous incisors of the lower jaw are the last to erupt, on the 17th–19th day. At that time, the deciduous canines appear. The replacement of the deciduous by permanent

incisors is completed at about the age of 4 months, and the third and final molar of the lower jaw erupts at an age of about 5 months. The times of eruption of deciduous teeth and the order of their replacement by the permanent ones is related to lactation, protracted feeding of the pups, and the time of their transition to an independent life.

Young jackals grow quickly. At the age of two days their weight is 201–214 g, at one month, from 560–726 g, and at 4 months, 2700–3250 g. Young caught at the beginning of September weighed 4200–4370 g, and by the beginning of October, their weight reaches $\frac{3}{4}$ of adult weight (Chernyshev, 1958).

The jackal molts twice yearly—in spring and in autumn. In the Trans-Caucasus and Tadzhikistan, the spring molt begins in the middle to end of February, in warm winters, in the middle of that month; in cold winters, it starts in mid-March and ends at the beginning to middle of May. In healthy animals, pelage replacement extends for 60–65 days in spring. Weak and sick animals do not succeed in completing molt during the entire summer; at the beginning of winter, half of the coat consists of spring–summer hair and half is winter fur (Dzhanashvili, 1947).

Spring molt starts with the head, the anterior and posterior limbs, then spreads to the sides, back, chest, belly and rump, and the last to molt is the tail. After spring molt, only scattered coarse guard hairs remain on the skin and underfur is absent. Autumn molt occurs from the middle of September. Shedding of summer pelage and growth of winter guard hairs and underfur take place simultaneously. Autumn molt starts with the rump and tail and spreads to the back, sides, belly, chest, limbs and head. Full winter fur has grown out by the end of November (Chernyshev, 1958). In the Caucasus, the skin is prime from November to March (Vereshchagin, 1947).

Enemies, diseases, parasites, mortality, and competitors. Earlier, enemies of the jackal everywhere were the tiger and leopard. At the present time, the first is extinct in the jackal's range, and the second is extremely rare. The leopard hunted jackals especially frequently. At the same time, jackals regularly fed on the remains of these cat's prey, and once, in Tigrovaya Balka, they ate a dead tiger. The wolf also should apparently be considered an enemy.

Its serious competitors everywhere are the jungle cat, red fox, wolf, and in the Trans-Caucasus, the forest wildcat [*Felis sylvestris*], and to a lesser degree, the recently acclimatized raccoon [*Procyon lotor*] as well. In Middle Asia and Kazakhstan, the steppe wild cat [*Felis libyca*]

is also a competitor. The small number of red foxes occurring in tugais may explain the abundance of the jackal there (Chernyshev, 1958). At the same time, in deserts and foothills, red fox and wolf apparently oust the jackal. Usually, where there are many wolves, jackals are absent, and vice versa.

Among the infectious diseases of jackal, carnivore distemper and rabies are established (Sludskii, 1954; Chernyshev, 1958). Epizootics of carnivore distemper in the winter of 1948–49 in Tadzhikistan (Tigrovaya Balka) affected not only jackals, but was also observed among shepherd and hunting dogs, the majority of which died. In southwestern Tadzhikistan, of 9 jackals examined, leishmania was found in liver and spleen smears of three, and was supposedly identified as Donovan's leishmania, which induces visceral leishmaniasis in humans. Jackals infected with leishmania suffered little from this infection (Latyshev and others, 1947).

Jackals are heavily infested with helminths. In southwestern Tadzhikistan, 15* species of cestodes, roundworms and acanthocephalans were discovered: *Sparganum mansoni*, larval form of *Diphyllbothrium mansoni*, *Taenia hydatigena*, *Taenia pisiformis*, *Taenia ovis*, *Hydatigera taeniaeformis*, *Diphylidium caninum*, *Mesocostoides lineatus*, *Ancylostoma caninum*, *Uncinaria stenocephala*, *Diocotophyme renale*, *Toxocara canis*, *Toxascaris leonina*, *Dracunculus medinensis*, Filariata gen. sp., [and] *Macracanthorhynchus catulinum*. Jackals infect water bodies with the parasitic worm larvae (*D. medinensis*) and may be responsible for dracunculosis in humans (Chernyshev, 1954). Moreover, they play some role in the spread of coenurosis of sheep and large horned cattle. In Uzbekistan, 10 species of helminths were found in the jackal, of which, in addition to 7 species mentioned for animals in Tadzhikistan (No. 6–12, see above), were found: *Spirocerca lupi*, *Rictularia affinis* and *R. cahirensis* (Irgashev, 1958).

Jackals in Tadzhikistan are infested with ticks in April–September, while in November–February, these parasites are only found in few individuals and in small numbers. The following species of ticks were found: *Ixodes* sp., *Rhipicephalus turanicus*, *R. leporis*, *R. rossicus*, *R. sanguineus*, *R. pumilio*, *R. schulzei*, *Rhipicephalus* sp., *Hyalomma anatolicum*, *H. scupense*, *H. asiaticum*, *Hyalomma* sp. Most frequently, *R. sanguineus* parasitizes the jackal in great quantities. The role of jackals in nourishing and spreading ticks is great. Four flea species are

*16 are listed—Sci. Ed.



Fig. 43. Track of jackal on silt. "Tigrovaya Balka", preserve at Pyandzh, Tadzhikistan. 15 October 1960. Photograph by A.A. Sludskii.

known on jackals: *Pulex irritans*, *Xenopsylla nesokiae* (a flea of the bandicoot rat), *Ctenocephalides canis*, *C. felis* and one species of louse—*Trichodectes canis* (Chernyshev, 1954).

In severe deep-snow winters, jackals often die from emaciation and exposure. In Azerbaidzhan, in severe winters, after the large lakes are covered with ice, jackals penetrate far into the dense growths of reeds and cattails and stay in them during the entire frozen period, not going to shore. At times of sudden thaws, they are stranded on the ice and die. Thus, in December 1946, when a thaw commenced, the animals which were living in the reeds were isolated from the land by water and drowned (Vereshchagin and Dyunin, 1949). In the severe winter of 1948–49 at the Shil'yansk lakes, as a result of sudden thawing, the animals became isolated from the shore and drowned at the borders of the impassable flooded reeds in their attempts to reach dry land. Other cases were observed when jackals, failing to reach the shore, remained starving for a long time on intact sections of ice (Pavlov, 1953). Near the Caspian Sea jackals sometimes die in great numbers in autumn and winter *moryan** which quickly fill coastal thickets, and in times of floods. Possibly, they also suffer from fires in the turgais and reeds.

*Violent on-shore storm — Sci. Ed.

Population dynamics. These are little studied. Judging by the data of fur buyers, the number of jackals is subject to considerable fluctuation. Thus, in Turkmeniya, fur purchases varied by nearly 3–4 times during the period from 1950 to 1956 (1400–5500 items). They fell especially greatly in 1954—to 1430—following the severe winter of 1953–54. Fur purchases considerably increased in 1956, reaching 5427 skins, following 1955, a year which was favorable for reproduction because of abundant food.

In Tadzhikistan, minimal fur purchases during the ten years was in 1951—258 pieces after the severe winter of 1950–51, and the maximum, as in Turkmeniya in 1956—1403 skins. In Tadzhikistan, fur purchase, and consequently the number of jackals, fluctuated approximately by six times. In the lower Amu-Dar'ya in the decades of the 30's–50's the catch of jackal skins varied by 2 times and was also related to the degree of severity of winter. In the south of Kazakhstan, jackals were relatively common in the 20's and 40's of the present century, during periods when there was much carrion in the desert.

In 1926–1929 in Kazakhstan, from 100 to 250 jackal skins were obtained; at the beginning of the 30's, this number dropped to 25–30 pieces; after which a few individuals were caught; but in 1942–1945 the number of jackals started to increase. By 1947, jackals were common in the most southerly regions. In this year, 104 jackal skins were tanned in Kazakhstan. In the following years, their number again dropped. However, these changes were mainly connected with their migrations from the south.

Field characteristics. The jackal is half the size of the desert wolf and nearly twice as large as the desert red fox, and is high in the limbs. Ears are erect, but more blunt than those of foxes. Tail short and 1/3 the body length.

Feces are sausage-like, and are found in noticeable piles, as the animal leaves them in one and the same place for several times. It often howls. The howling is similar to a wail, and can be rendered by the sounds "Ai-yai! Ai-yai!"—high, whimpering. It is similar to that of dogs, but is higher and more varied and is differentiated by a "plaintive" intonation. To the howl of one jackal, those nearby answer (A.S.).

Practical Significance

The jackal is a fur-bearer, but its fur is of low value, characterized by sparse, coarse pelage and has a monotonous unbeautiful color. Already

in the last century the jackal was utilized (Silant'ef, 1898). In the Trans-Caucasus, in the Zakatal area, 300 jackals were captured in 1896, and in the B[olshoi] Trans-Caspian district, the jackal was hunted in many jurisdictions, and in Mervsk, in the eighties, about 200 animals were caught yearly. The total taken in Russia in that period was more than ten thousand jackals. Jackal skins were sent to the Nizhegorod fair (they were not sent to other fairs) in the following numbers:

Year	1880	1881	1883	1884	1885	1886	1887
Number of skins (in units)	8000	10,000	3000	4000	4000	3000	2800
Year	1888	1889	1890	1891	1892	1893	
Number of skins (in units)	3000	3000	3500	4000	4000	3000	

In the decade of the 20's in this century, the following numbers of skins of this animal were tanned in Trans-Caucasus (Markov, 1934):

122 Years	1924— 1925	1925— 1926	1926— 1927	1927— 1928	1928— 1929	1929— 1930	1931	1932
Number of skins	4386	6159	4027	11793	9334	13635	11819	13384

In Middle Asia and Kazakhstan lesser amounts of skins were prepared (Tables 7, 8).

In the entire Soviet Union, at the beginning of the 30's of the current century, about 20–25 thousand were tanned yearly (Naumov and Lavrov, 1941; Kaplin, 1960). However, the stocks of this animal were significantly underutilized. In 1940, 10.4 thousand furs were processed. At present, it is possible to increase the size of the jackal take by a minimum of three-fold. The world production of jackal skins in 1907–1910 was 20–25 thousand items (Asia 5.0, Europe 5.0, Africa 10.0; Kaplin, 1960). Previously, the majority of skins tanned in the USSR were sent abroad, mainly to the USA. Since 1949, the skins have been utilized inside this country.

The skins are not graded according to a fur standard, though those obtained from the Transcaucasus possess coarser fur of reddish-brown color, while those from Middle Asia differ in their softer paler fur. They are divided into four sorts, and used in the manufacture of cheap collars, women's coats and *dokhas* [fur-coats]. They are usually dyed. Suede is prepared from the skins of grade IV.

A special harvest of jackals does not exist. The animal is caught incidentally to the hunting of other animals, by means of traps or by

Table 7. Jackal skin purchases in Middle Asia and Kazakhstan (in units)

Union Republics	Years					
	1924-1925	1925-1926	1926-1927	1927-1928	1928-1929	
Uzbek and Tadzhik SSR	1518	—	2543	2677	2416	
Turkmen SSR	—	—	No information			
Kirgiz SSR	—	—	2	1	3	
Kazakh SSR	—	—	248	154	111	

Table 8. Jackal skin purchases in Middle Asia in the period 1948-1958 (in units)

Union Republics	Years										
	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
Turkmen SSR	2756	1989	2065	1875	1505	1637	1430	3018	5427	3937	2705
Uzbek SSR	—	—	6161	4618	4596	4563	4256	6009	4684	4684	3268
Tadzhik SSR	—	—	—	258	576	918	880	857	1403	764	534

shooting while on drives. When traps are employed, they are set near carrion, on garbage dumps (in such places the beast pays little attention to the odor of metal) and in shallows along shores; as a bait, a large live fish is tethered on a *kukan** (string).

In the Trans-Caucasus, jackals are hunted with large fishing hooks which are suspended from a metallic cable or wire at a height of 75–100 cm from the ground, in such a manner that the predator can reach it only by jumping. The hook is baited with a piece of carrion. On seizing the bait, the animal is hooked by the lip or jaw (Markov, 1934). The jackal is snared by wire nooses placed on their trail. Poisons are also utilized (see above concerning food).

- 123 The jackal is a serious pest of the agricultural and hunting economies. In the Trans-Caucasus, "jackals must be considered the most harmful destroyers of game" (Dinnik, 1914), causing the most severe losses to the hunting economy, not excepting the wolf (Markov, 1934). They destroy, in large quantities, newborn roe deer, hares, and nutria as well as pheasants, francolins, gray partridges, little bustards and great bustards during overwintering, and waterfowl (Satunin, 1915; M. Pavlov, 1953; Katubadze, 1956; Burdzhanaдзе, 1959). The jackal is a dangerous enemy of the nutria, completely destroying them in shallow water bodies (M. Pavlov, 1953). They are very harmful to the muskrat trade. In the Amu-Dar'ya delta, during the winter of 1948–49, in the feces of this predator the remains of muskrat constituted 12.3% of all examined samples. In particular places, jackals destroyed up to 71% of the muskrat houses, of which about 16% froze and became unsuitable for occupation (Pokrovskii, 1953). It causes also great harm to the muskrat trade in the Khorezma district where muskrat houses are easily accessible to it. The jackal also damages the muskrat harvest by eating muskrats caught in traps, and skins hung up for drying (Kostin, 1956).

The jackal is very harmful to poultry and carries off lambs and kids (Satunin, 1915). It eats ripe grapes in such quantities that earlier, in the Bol. Lenkoran vineyards, owners removed the flowering branches hanging near the ground because the fruits will in any case be eaten by jackals (Satunin, 1915). The jackal destroys watermelon and melon. In one melon field in Tadzhikistan, the jackals destroyed, ate and spoiled 70 ripe melons in one night (Chernyshev, 1958). In the Trans-Caucasus and Middle Asia, the jackal, as much as the red fox and wolf, serves as a carrier of rabies in nature.

*Local word?—Sci. Ed.

Cases are known in which rabid jackals have run into villages, where they have bitten man and domestic animals (Bikhner, 1905). The value of jackals as eaters of small rodents and insects is inconsiderable.

The jackal may be killed the year round, until such time as their numbers proceed down to a minimum. In all republics, there exist decrees permitting their hunting throughout the entire year. (A.S.)

WOLF

Canis lupus Linnaeus, 1758

- 1758. *Canis lupus*. Linnaeus. Syst. Nat., Ed. X, 1, p. 39. Upsala, Sweden.
- 1792. *Canis lupus albus*. Kerr., Animal Kingdom, p. 137. Lower Yenisei.
- 1804. *Canis lupus communis*. Dwigubski. Prodrum faunae Ross., p. 10. "Russia"—apparently, the northern forested section of European Russia (the steppe wolf Dwigubski inserts separately; see below).
- 1804. *Canis lupus campestris*. Dwigubski. Ibidem, p. 10. Cis-Caucasian steppes.⁹
- 1831. *Canis pallipes*. Sykes. Proc. Zool. Soc. London, p. 101. Deccan, India.
- 1847. *Lupus laniger*. Hodgson. Calcutta Journ. Nat. Hist., 7, p. 474. Tibet. Nec *Canis laniger* H. Smith 1840 (domestic dog of Puget Sound Indians).
- 1863. *Canis chanco*. Gray. Proc. Zool. Soc. London, p. 94. "Chinese Tatar". Tibet.⁹
- 1875. *Canis arundinaceus*. Karelin. Tr. SPb Obsch. Estestvoisp., 6, p. 81. South Ural steppe. Nomen nudum.
- 1882. *Canis lupus* var. *desertorum*. Bogdanov. Ocherki prirody Khivinskovo oazisa i pustyni Kyzylkumy, p. 30, Kyzylkum.
- 124 1907. *Lupus filchneri*. Matschie. Wiss. Ergebn. Exped. Filchner nach China u. Tibet, 10, 1, p. 153. Si-ning to the east from Kukunor.
- 1907. *Lupus karanorensis*, Matshie. Ibidem, p. 157. Khala-chu in Gobi (a little west of Sa-chzhou. V.H.).
- 1907. *Lupus tschiliensis*. Matschie. Ibidem, p. 160. Shangaiguan' on shore of Lyaodunsk gulf.

⁹For reasons, see later in section "Geographic Variation".

1911. *Lupus altaicus*. Noak. Zool. Anz., 35, p. 465. Teletskoe lake and Chulyshmansk mountains, Altai.
1922. *Canis lupus* var. *orientalis*. Auct. Dybowski. Archiv Tovar, Naukow. Lwowe, 1, p. 350. Forest of Eastern Siberia. Nec *orientalis* Wagner 1841. Nomen nudum.
1922. *Canis lupus* var. *argunensis*. Dybowski. Ibidem, p. 350. Steppes of Dauriya. Nomen nudum.
1922. *Canis lupus* var. *kamtschaticus*. Dybowski. Ibidem, p. 350. Kamchatka. Nomen nudum.
1923. *Canis lupus cubanensis**. Ognev. Biologicheskije izvestiya, 1, p. 114. Mountains of Maikop area, Western Caucasus (district of present Caucasian preserve, at sources of Kuban tributaries—Laba and Belaya).
1923. *Canis lupus turuchanensis*. Ognev. Ibidem, p. 115. Turukhan territory (right bank of lower Yenisei).
1926. *Canis lupus dybowskii*. Domaniewski. Annal. Zool. Musei Polonici Hist. Nat., 5, p. 52. Kolygino, southwestern coast of Kamchatka.
1929. *Canis lupus bactrianus* Laptev. Opredelitel' mlekopitayushchikh Srednei Azii, 1, p. 51. Surkhandar'insk region.
1930. *Canis lupus coreanus*. Abe. Journ. Sc. Hiroshima Univers. Zool., 1, p. 33. Near Seoul, Korea.
1931. *Canis lupus hattai*. Kishida. Lansania, 3, No. 25, p. 73. Hokkaido, Japan.
1935. *Canis lupus rex*. Pocock. Proc. Zool. Soc. London, p. 659. Hokkaido, Japan.
1936. *Canis lupus dorgostaiskii*. Skalon. Izv. Gos. protivochumn. inst. Sibirii i Dal'nevo Vostoka, 4, p. 193, Borzya, Eastern Trans-Baikaliya.
1951. *Canis lupus hajastanicus*. Dahl. Dokl. Akad. nauk Armyansk. SSR, 14, No. 3, p. 91. Vicinity of Erevan, Trans-Caucasus. (V.H.).

Diagnosis

Body length of adults not less than 90 cm, tail length about half that of body. Length of skull more than 200 mm. Arciform line formed by anterior border of both nasals, has no process in middle (along line of suture between nasal bones). At anterior inner sides of auditory bullae,

*In Russian original, misprinted as *cubanensis*—Sci. Ed.

swellings in form of ridges found on basioccipital. Cingulum on outer side of first upper molar narrow and weakly developed, with constriction or gap in middle. (V.H.).

Description

The wolf is a slender, well-proportioned, powerful animal. It has a strong trunk with sloping back, with high shoulders and a lower, but strong and wide croup. The rib cage is large, deeply descending, the abdomen is pulled in and the neck is powerful and muscular. The limbs are long and strong, the paws are relatively small and the digits are tightly compressed ("in a lump").

125 Head large, heavy, with strong jaws, a long but not pointed, muzzle, and broad forehead. Eyes are widely separated and small. Supraorbital arches are well developed and therefore the eyes appear to be seated deeper as if slightly squinting, even somewhat slanting. Ears relatively small, triangular in form with pointed tip, directed forward and widely separated, and therefore the wolf's head looks especially "broad in the forehead". The animal usually carries it [the head] a bit hanging, not higher than the level of the back, and appears slightly stooping, with its high shoulders. Only the watchful wolf raises its head high.¹⁰

Tail fairly large, fluffy, hanging down to the tarsal joint. It looks as if broken at the base and in the standing and calmly moving wolf, it hangs directly downwards. Only during fast galloping does the wolf somewhat raise it, and carries it "outstretched" but not higher than the back level. In the live animal, the tail moves little and looks very heavy (in hunting language it is aptly called a "billet" [chunk of wood]). In known psychic states (glad excitement, affection) the wolf wags its tail, although not entirely as the dog does. When in fear, it puts its tail between its legs as does the dog. Claws black. Eyes yellow. Teats, 5 pairs.

The winter fur is very dense and fluffy with short underfur and long, quite coarse guard hair. The tail is very densely covered with long hairs, which are considerably shorter at the root than along the remainder of its length. In the south, the fur is scarce and coarser, in the mid-zone, dense and luxuriant, but fairly coarse, and in the north it is longer, denser, more luxuriant and softer.

¹⁰The wolf is an animal of high psychic [*sic*] level, and possesses rich mimicry. Special study showed that the wolf has ten expressions of the "face" corresponding to specific psychic conditions.

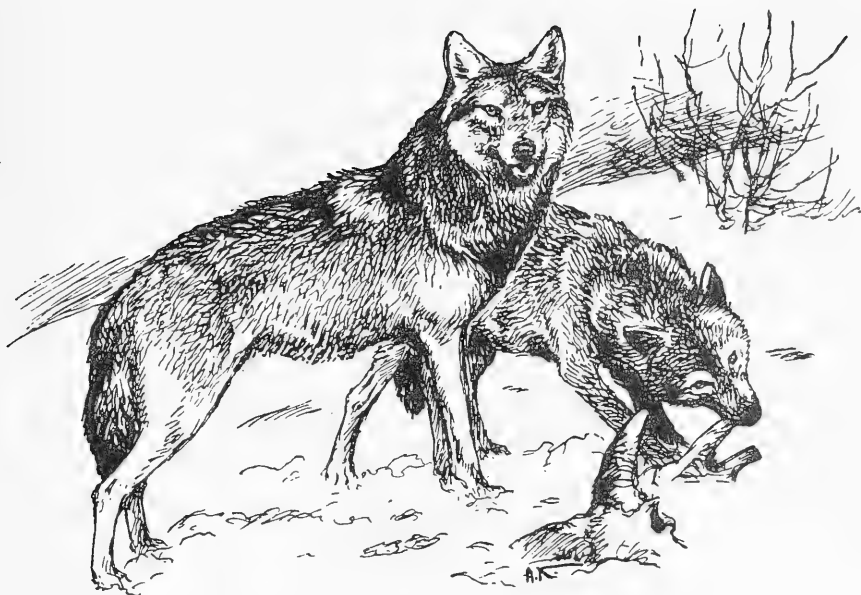


Fig. 44. Wolves, *Canis lupus* L. Sketch by A.N. Komarov.

The longest hairs are found on the back, mainly on its anterior part, and on the neck. On the shoulder there is usually a region of especially long hairs, and on the upper part of the neck the long hairs form a kind of crest. The anterior part of the head, including the forehead, is covered with short hairs, while on the remaining part, the hairs are longer. On the cheeks, the hairs are elongated and form "tufts"—small side-whiskers. The limbs, to elbows and a little above the calcaneal joint, are covered by short, elastic, closely adjacent hairs. The ears are covered with short hairs and strongly project from fur. The summer fur in all latitudes is much more sparse and shorter than that of winter, and is coarse and harsh.

126 Coloration is monotone, in various parts of the country monotypic, and geographically varies comparatively little. Individual variation is fairly great, but affects details, while the general color tone and distribution of colors are constant. Seasonal differences in coloration occur, but are not sharp, and vary in different parts of the range. In some areas, in connection with color fading in winter, the color somewhat (sometimes considerably) changes (brightens). Among Soviet wolves, melanists, albinos and erythristic are found, but are very rare. Their appearance sometimes results from hybridization with domestic dogs.

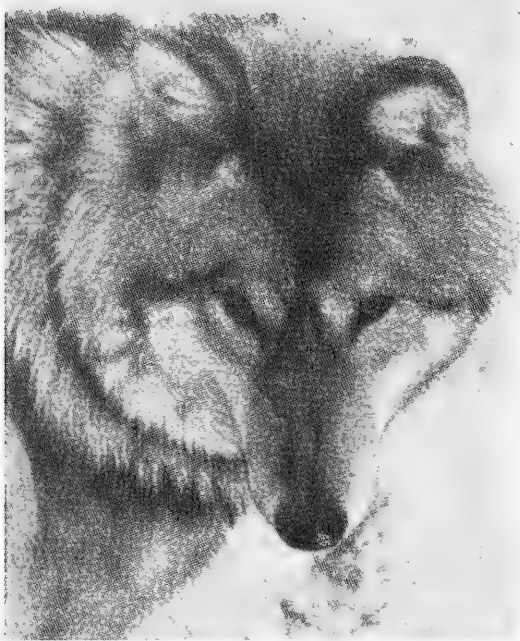


Fig. 45. Head of adult male wolf. Krasnoyarsk territory. Photograph by V.V. Kozlov.

The wolf of southeastern North America, *C. l. niger*, has diphasic coloration—normal and black.

Sexual differences in color are absent. The coloration of the adult Middle Russian wolf in summer fur is composed of a mixture of ochreous and rusty ochreous tones with light gray. Over the entire skin, especially on the surface of the back, there are some admixtures of black, as a result of the black ends of the guard hairs. The muzzle, approximately to the level of the eyes, is pale ochreous-gray, the circumference of the lips and the lower parts of the cheeks are white. The space between eyes, the forehead, top of head, occiput and the region under the eyes and between eyes and ears are gray, only with a light reddish film. Around the eyes there are small ochreous rusty fields (rings). The backs of the ears are rusty-ochreous with a mixture of blackish-brown, and their inner surfaces are covered by dirty white hairs. The chin and throat are pure white. The neck is ochreous, somewhat overlaid with black (dark ends of hair) on the upper side.

Long, dark (black) guard hairs along the spine form a well-defined black pattern in the form of stripe which is especially bright and broad in the anterior part of the back. A quite large amount of hairs with black tips is also present on the shoulder blades, and in part on the upper part of chest, and the sides on the posterior part of the body. However, a dark frosting in the form of obvious "dorsal saddle" is not formed. The coloration of the sides of the body and the outer parts of limbs is pale dirty ochereous and the inner sides of the limbs are white. Belly and inguinal region are white with an ochereous frosting. On the anterior side of the fore legs there is usually a sharply outlined and well-defined longitudinal stripe.

Coloration of the tail corresponds to that of the sides of the body—bright dirty ochereous. On the dorsal side, especially on the basal third, there is a strong admixture of dark (black, black-brown) hairs; the tip of the tail is often black. Hair length in the middle of the back is 60–70 mm.

The winter fur retains in general the main tones and also distribution of the variously colored parts. However, general coloration is brighter as a whole in connection with the fact that the underfur is more prominent; the tinge of black hairs on this background is more striking, appearing as a sort of weak dorsal saddle; ochereous tones appear weaker
 127 and the smoky-gray is more strongly developed. If in some individuals, the ochereous tone is clear and quite intensively developed, in some others it is weak and the animal looks very light and gray. The length of the guard hairs on the shoulders does not usually exceed 90 mm, but may reach 110–130 mm.

Age variation in characters of the fur and in coloration is in the first year well expressed. Young wolves in their first pelage are covered with dense, short (in the middle of the back 20–30 mm), very soft "downy" fur of dark-brown or grayish-brown color. This coloration is quite evenly distributed on the entire body. The region around the eyes and the inner surface of the body are somewhat lighter, while the muzzle and the lips, on the contrary, are darker. On the belly the hairs are dirty gray with brownish tints and on the chest, between the anterior limbs, there is a lighter area. The color of the tail, which is covered by short hairs, corresponds to that of the trunk. A white tip on the tail never occurs. The claws are light.

This juvenile pelage quickly begins to change and at the end of summer the young wolf, still far from attaining the size of the adult (not less than two times smaller) has light dirty grayish-ochereous fur, coarse and sparse. Reddish tone is not developed and black guard hairs are



Fig. 46. Adult male desert wolf, weight 31 kg. Betpak-Dala desert, Kazakhstan. 24 May 1955. Photograph by A.A. Sludskii.

absent or few. This coloration is quite evenly distributed on the body and the light or, on the contrary, dark areas are not differentiated. The claws become black.

From this second pelage, the hairs of which grow greatly by autumn, the young (“growing”)* wolf passes into the first winter pelage. It corresponds to the winter fur of adult animals, but differs in the greater monotony of the grayish dirty-ocherous color with less development of black and reddish. The color of the wolf in the second year (“yearling”)**, both in summer and especially in winter, does not differ from that of older animals.¹¹

*The Russian word *pribylnoi*, while literally meaning “growing” or “increasing”, is best considered the equivalent of “juvenile”—Sci. Ed.

**Russian, *pereyarka*—Sci. Ed.

¹¹Numerous hunters have remarked on age differentiation of wolves on the basis of color, as well as have the notes of old authors (Lorents, 1890; Sabaneev, 1877 and others) but these are not reliable and invalid (Ognev, 1931; Heptner, 1947; and Heptner and Turova, 1951).

The skull of the wolf is characterized by massiveness and generally large dimensions. This is the largest form in the family. The facial portion, in connection with strongly developed teeth, is relatively long and massive; the cranial part of the skull is comparatively small and weakly swollen, and is considerably shorter than the facial part, and the braincase is relatively small. The nasal bones are long, their posterior ends extending to the level of the orbits. Each bone, at the front, is notched in an arciform manner in such a way that a common protuberance is not formed at the line of contact of both bones anteriorly (Fig. 15). Along the whole length of the line of contact of the nasal bones with each other a longitudinal depression (groove) is present.

The premaxillae gives off a large dorso-posterior process which, however, does not reach the frontal bones. The posterior borders of nasals and maxillary bones lie approximately on the same level. The zygomatic arches are massive and widely separated, especially posteriorly. The supraorbital processes are large and massive and strongly protrude laterally. The facial portion is quite elevated anteriorly and in the middle and posterior parts of the nasal bones the profile is somewhat concave and the forehead abruptly rises upwards, reaching its greatest height in the region of the supraorbital processes.

The frontal region is wide, slightly concave in the middle and convex on its margins. Behind the supraorbital processes, the cranium is compressed. The sagittal crest is well developed; it bifurcates anteriorly, demarcating the frontal area from the sides and continues to the border of the posterior part of supraorbital processes. The occipital crest is strongly developed and overhangs the occipital region of the skull. The bones of the auditory bulla are of moderate size, thick-walled, and their anterior inner parts are not directed to each other, but diverge laterally; in this part, at the base of the jugal, are found small elongated ridges or swellings.

The tooth row is very powerful, carnassial teeth are massive and the canines are strong, relatively short, but with a wide base.

Age variation of the skull is very great and is reflected mainly in the development of the crests, the relative increase in the facial portion, increased convexity of the frontal region, and the increased constriction of the cranium behind the orbits.

The wolf cub skull still possessing deciduous teeth is characterized by the following characters: facial region of the skull is very short and much shorter than the cranial; width of the skull in the region of carnassial teeth is great; zygomatic arches are situated very close and

are weak; cranial portion of the skull is relatively large and swollen; crests are absent; contour of the braincase region is circular (no projections in the upper part of the occiput); no constrictions behind the orbits; supraorbital processes not defined; frontal region rises slightly, and projections in this part of the skull are absent; auditory bullae are relatively large and more rounded; the coronary processes of the lower jaw are sharply curved backwards; and the angular processes are small.

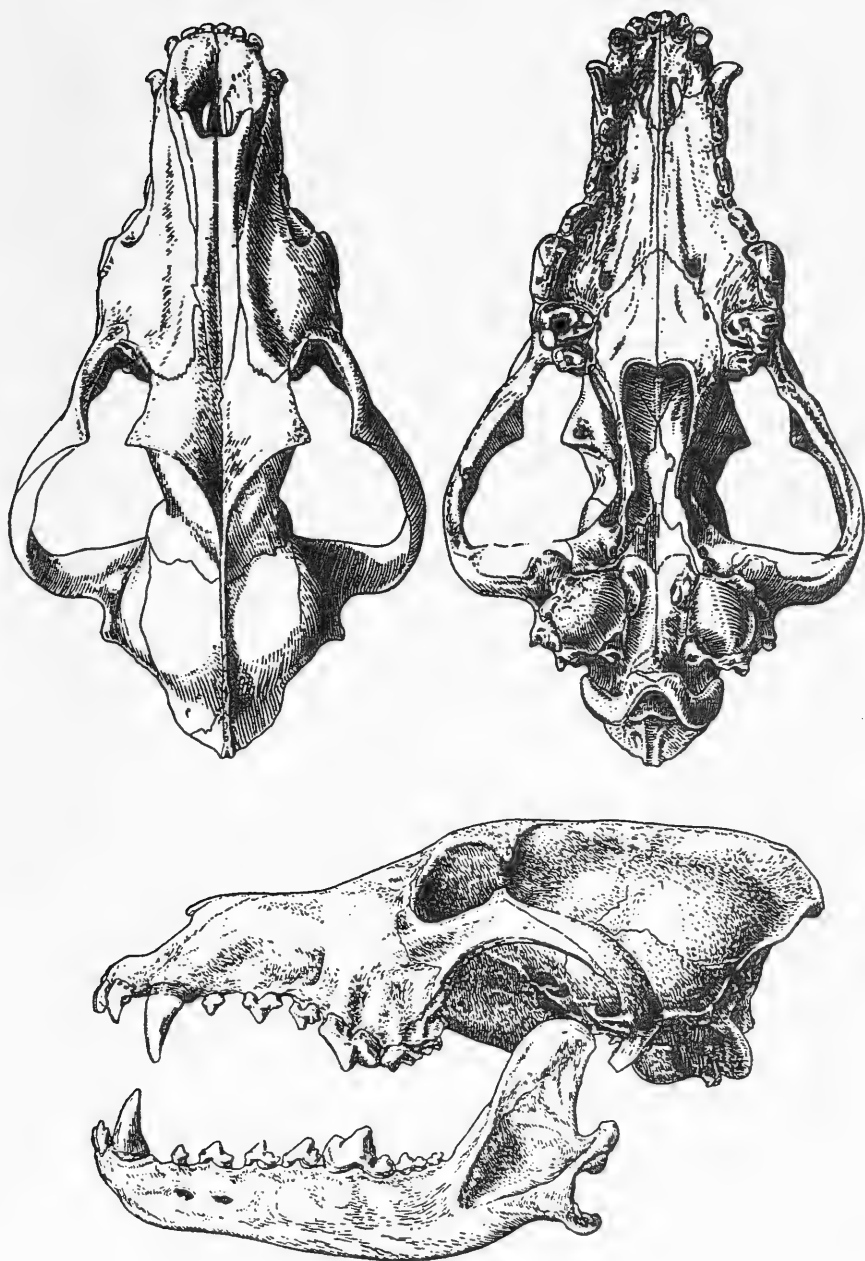
The skull of the juvenile wolf immediately after tooth replacement (in the first autumn of life) has a skull that appears similar to that of the adult animal, but differs in the following characters: nasal portion is somewhat shorter; skull width in the region of carnassial teeth is somewhat greater; zygomatic breadth is less; region of the braincase is relatively a little longer; crests are absent, and only in the occipital region is the posterior part of sagittal crest defined; supraorbital processes are small, short and weakly pointed; constrictions behind the supraorbital processes are less, and bones of the auditory bullae are relatively larger.

The skull of the very old wolf, as compared to that of the adult, is characterized by a relatively still more elongated facial portion, massive and very widely separated zygomatic arches, high and very greatly
 130 developed crests, a wider forehead with greater distance between the tips of the supraorbital processes, and sharper constriction of the braincase behind the supraorbital processes.

Sexual differences in the skull are manifested only in somewhat smaller average dimensions of female skulls. Age changes in their skulls are manifested in the same way as in males.

The length of the intestine of adult Middle Russian wolves (2 specimens) is 460–575 cm, that of the juveniles 7–8 months old is 390–420 cm (3 specimens); the ratio to body length in the former is 4.13 and 4.62, while in the latter, it is 3.64 and 3.86. The relative weight of the heart (Hesse index) varies from 7.32 to 13.07; in young it is apparently less than in old (Heptner and Morozova-Turova, 1951). The length of the intestine (without the caecum) and the corresponding index of two adult males from the extreme north (tundra of Arkhangel'sk district—Taimyr) are 698 cm and 1 : 5.3 and 490 cm and 1 : 4.0. Their heart weight is 800 gm and 16.4% (?) and 437 gm and 9.34 % (from material of V. Makridin).

The diploid number of chromosomes is 78, the fundamental number, 80 (Matthey, 1949).



The dimensions of wolves are subjected to geographic variation. Body length of an adult wolf ranges between 105 and 160 cm; tail length between 29 and 50 cm (usually from 40 to 50); hind foot length is about 220–250 mm; and ear height is about 110–190 mm. Height at the shoulders is 80–85 cm, and it may reach 100 cm.

Weight of adult Middle Russian wolves usually fluctuates between 32 and 50 kg. Females are not usually so massive as males, of somewhat smaller dimensions, and their weight is considerably less than males. Average weight of females constitutes about 80–85% of average male weight.

Information on the weight of wolves available in the literature, especially old hunter's and popular tales, are exaggerated. This is explained by the fact that they are mostly based on the determination of the weight of particularly large animals "by eye". Recently, in some districts, mainly in the middle zone of the European part of the USSR, accurate data on the weight of large series of animals appeared (see section on "Geographic Variation"). These figures make us deal cautiously with many of the old data on the average weight of wolves from different parts of the range.

Nevertheless, huge wolves are sometimes found in some places. Such animals, however, are very rare. In Middle Russia in general form, the maximum weight of wolf is given as 69–79 kg (Ognev, 1931) and 80 kg (Zvorykin, 1939).

Separate more accurate cases, recently verified, are the following: In Saratov district, a wolf weighing 62.4 kg was recorded (Ognev, 1931); in the forest zone of the European part of the country, 69 kg (A.A. Sokolov); in the districts around Moscow, a male weighing 76 kg is known—this was the largest one among 250 animals killed by the famous wolf-hunter V.M. Khartuleri (Heptner and Morozova-Turova, 1951). In the Ukraine, animals of 92 kg (Lugansk district) and 96 kg are known (Chernigov district; Korneev, 1950; circumstances under which weight of these animals were determined are not known). In the Altai, a male weighed 72 kg (Afanas'ev et al., 1953). In the Zoological Museum of Moscow University, there is a mounted Middle Russian wolf (from F.K. Lorentz), which weighed about 80 kg ("5 poods") (V.G. Heptner).

Information from Vladimir district in recent years indicates that here there is a relatively high percentage of large animals. Of 641 wolves caught during the years 1951–1963 inclusive, 17 animals which attracted attention because of their particularly large size were weighed.

They were caught in Petushinsk, Muromsk, Sobinsk and Suzdal'sk regions and had the following weights (kg): Males—48 (February), 49 (January), 52 (February), 52 (November), 56 (February), 65 (December), 68 (January), 70 (March), 76.3 (March), 79 (January); Females—40 (March), 41 (February), 45 (February), 48 (November), 55 (December), 58 (March), 62 (January). Along with these, three adult wolves (older than two years), but from “the smallest” were weighed: males 32 and 36 kg (March, April, Gorokhovetsk region) and a female 30 kg (March; data of hunting inspection of the district—N.D. Sysoev).

Concerning the Altai animal, it is known that it had “little meat” in the stomach, but no other information was given. Sometimes the very large weights of individual animals are related to the fact that they were supposedly weighed with their stomach quite filled with food; recently some have averred that a large wolf can eat 10–15 kg (!) of meat. Just now this has been clarified, and information about the voracity of wolves is greatly exaggerated. Of 115 Voronezh wolves, only one had 2 kg of meat in the stomach, while all the rest had much lesser amounts (Merts, 1953). Of nearly 50 Saratov wolves, none had more than 3 kg of food in the stomach (V.G. Heptner). Therefore, the weight of some animals under all conditions very greatly exceeds the extremes of normal variation (V.H.).

Systematic Position

Within the genus *Canis*, which is considered here in its most narrow sense, *C. lupus* must be considered a more specialized progressive form. Its morphological specialization as a predator is, apparently, related to its adaptations for hunting large animals. Apparently, with this, i.e. with its group way of life in the course of the greater part of the year, are also related the progressive, highly developed, psychic characters of the wolf (the structure of the pack, the capacity for domestication, and so on). Obviously, we must evaluate the systematic position of the wolf in the widest interpretation of the genus (see characteristics of the genus and family). (V.H.).

Geographic Distribution

Almost all of Eurasia (except the extreme south and southeast) and North America (except the extreme south).



131 Fig. 48. Sole of front foot of a wolf caught in the Sobinsk region of Vladimir district. Winter fur. Natural size. Live weight of the animal 79 kg. Sketch from nature by A.A. Alyapushkin.

The range in the USSR constitutes a very great part of the species range and occupies nearly the entire territory of the country.

Geographic Range in the Soviet Union

The wolf is absent only on the Solovetsk islands, Franz-Josef Land, Severnaya Zemlya and the Karagin, Commander and Shantar islands. Sakhalin is also included in the range (Shrenk, 1858; A.M. Nikol'skii, 1889, Suprunenko, 1890); however, since the beginning of present century, it does not live there, and only occurs occasionally as a transient, crossing Nevel'sk Strait on ice. Wandering animals do not become established (V.G. Voronov and A.G. Voronov).

Concerning the Kuril islands, information in the literature is indefinite and contradictory and, to a considerable degree, erroneous. Wolves were recorded on Kunashir and, with doubt, on Iturup (Kuznetsov, 1949) and Paramushir (Podkovyrkin, 1950); wolves recorded on Shumishu (Sergeev, 1947) are simply feral dogs (Podkovyrkin, 1960). According to the most recent data, in the middle of the 60's, no wolves were found anywhere on the Kuril islands, and all records pertain to feral dogs, which, in particular, are present on Iturup, Urup, Shumishu, Kunashir and Paramushir (V.G. Voronov).

In the north, wolves are met with on Kolguev, Vaigach, and South islands of Novaya Zemlya, on White Island, on the coastal islands of the western (Nordenskiöld island), northern and northeastern Taimyr (in particular, Samuil island), on the Lyakhovsk islands and on the New Siberian archipelago—on New Siberia and Kotel'n (E.I. Shereshevskii) and Wrangel' island.

At the extreme limits of its range in the north, in particular in the northern Taimyr and on the islands to the east of Novaya Zemlya, the wolf occurs irregularly and as a transient, not even every year. Thus, 134 on Wrangel' island only one migration by three animals was known in 1938 (Manteifel', 1947). Since migrations here of foxes are known, this instance is probable although the width of Delong strait is more than 150 km.

In the Arctic zone, the distribution and intrusions of wolves are connected with the distribution and migrations of domestic and wild reindeer (see reindeer in vol. I). This applies to individual years as well as to considerable periods of time. Thus, wolves which fairly regularly inhabited the southern island of Novaya Zemlya have disappeared with the disappearance of the wild reindeer from this region and have not been met with for a long time there (see "Biology" section).

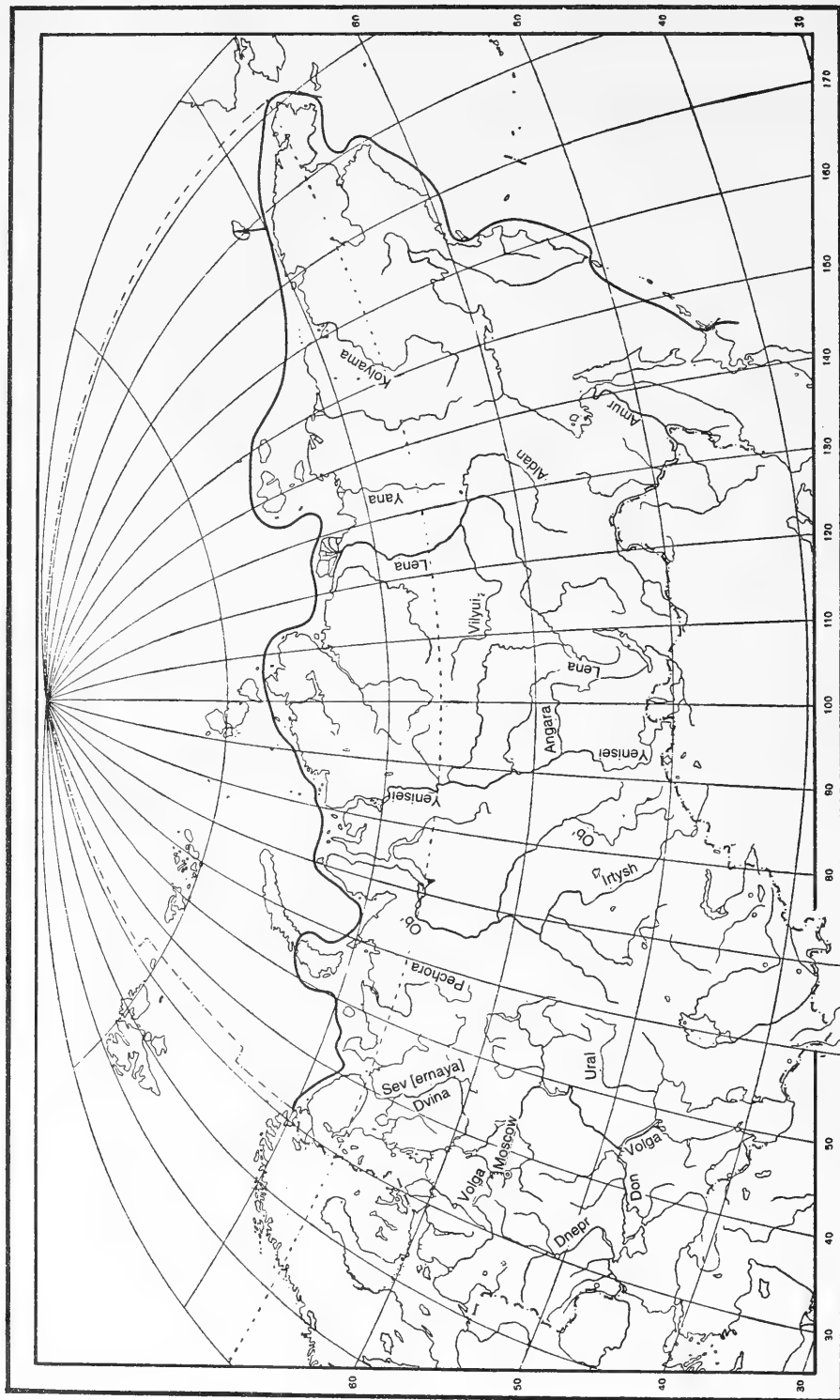


Fig. 49. Northern and eastern boundaries of the distribution of the wolf *Canis lupus* L. in the USSR. V.G. Heptner.

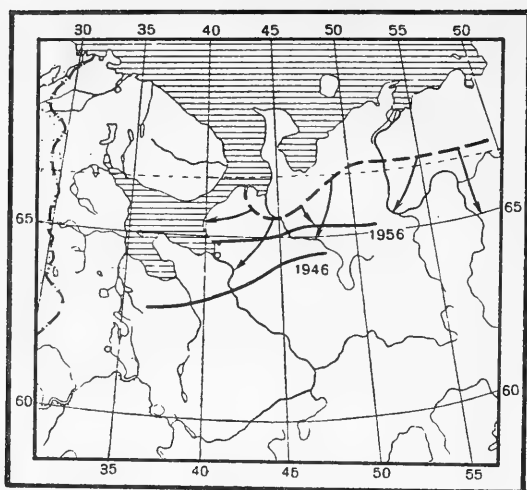
To the south of the designated northern boundary, the wolf is encountered everywhere, including the extremes of high mountains and deserts, though in very different numbers. The wolf is extremely rare, and absent in some places over considerable areas only in the taiga, which owing to its heavy snows and the relative poverty of food resources, represent the most unfavorable situation for the animal's life. When living conditions change, the wolf also occupies these districts. Thus, in the north of Arkhangel'sk district, in connection with clearing of forests, the spreading of stock-raising to the north, an increasing number of forest wolves are nowadays energetically moving northward into the taiga districts which were previously unavailable to them (Parovshchikov, 1959). In the last decades, due to felling, road construction, appearance of villages and similarly due to the disappearance in many places of its enemy—the tiger—the wolf occupied a considerable part of Ussuri taiga where it was previously absent and is quickly spreading northward (Abramov, 1954 and others).

A long time ago wolves were completely destroyed in the Crimea and were totally absent there for a long time. They appeared there during the Civil War, but they were again eliminated. During the Second World War and the first years thereafter the animals appeared again on the peninsula, but quickly disappeared.

Wolves have migrated across the ice to several islands in the northern part of the Caspian Sea, and at the time of seal hunting, attracted by the abundance of food (carcasses of killed animals), they go far onto the ice of the open sea (from the eastern shore, V.G. Heptner).

Geographic Range outside the Soviet Union

This comprises Japan (now extinct), the Korean peninsula, China southward to the Yangtze-kiang, the Mongolian Republic, Tibet, the Hindustan [Indian] peninsula to Bengal on the east and at least to Dharwar (about latitude 15°30' N. Lat., a little east of Goa) to the south, Baluchistan, Afghanistan, Iran, Iraq, the Arabian peninsula, the countries of the
 136 Levant and all of Europe. In Europe the wolf is exterminated in Ireland, England, France, Holland, Belgium, Denmark, Switzerland and in all of Central Europe. In the German Democratic Republic and even in the Federal Republic of Germany during the war and the post-war years, the appearance of few vagrant individuals was noted.



134 Fig. 50. The boundaries of distribution of forest wolf (solid line) and tundra wolf [broken line]* in Arkhangel'sk district. Arrows indicate direction of winter movements of tundra wolf to the south (after Parovshchikov, 1959).

In North America, the range of the wolf (reconstructed) occupies nearly the entire continent; on the south, to the southern border of the Mexican highlands (near 20° N. Lat.), and on the north, the whole Arctic archipelago. It also occupies the northern coast of Greenland and the western and eastern to 69° N. Lat. (Disko [Island], Godhavn and Scoresby Sound). Accordingly, the most northern point of the animal's occurrence is located only 700 km from the pole.

In the south, the range does not include the extreme margins of the western coastal parts of the continent, beginning at 41° N. Lat. in the south, both in the United States and in Mexico, and the coastal areas of eastern Mexico to the Rio Grande. The range also does not include the Queen Charlotte islands (it is on Vancouver Island) and the islands of the Bering Sea (although they are known to have crossed the ice to Saint Lawrence Island). The wolf is exterminated in a considerable part of the United States and several races are completely extinct. (V.H.).

*Not in original Russian—Sci. Ed.

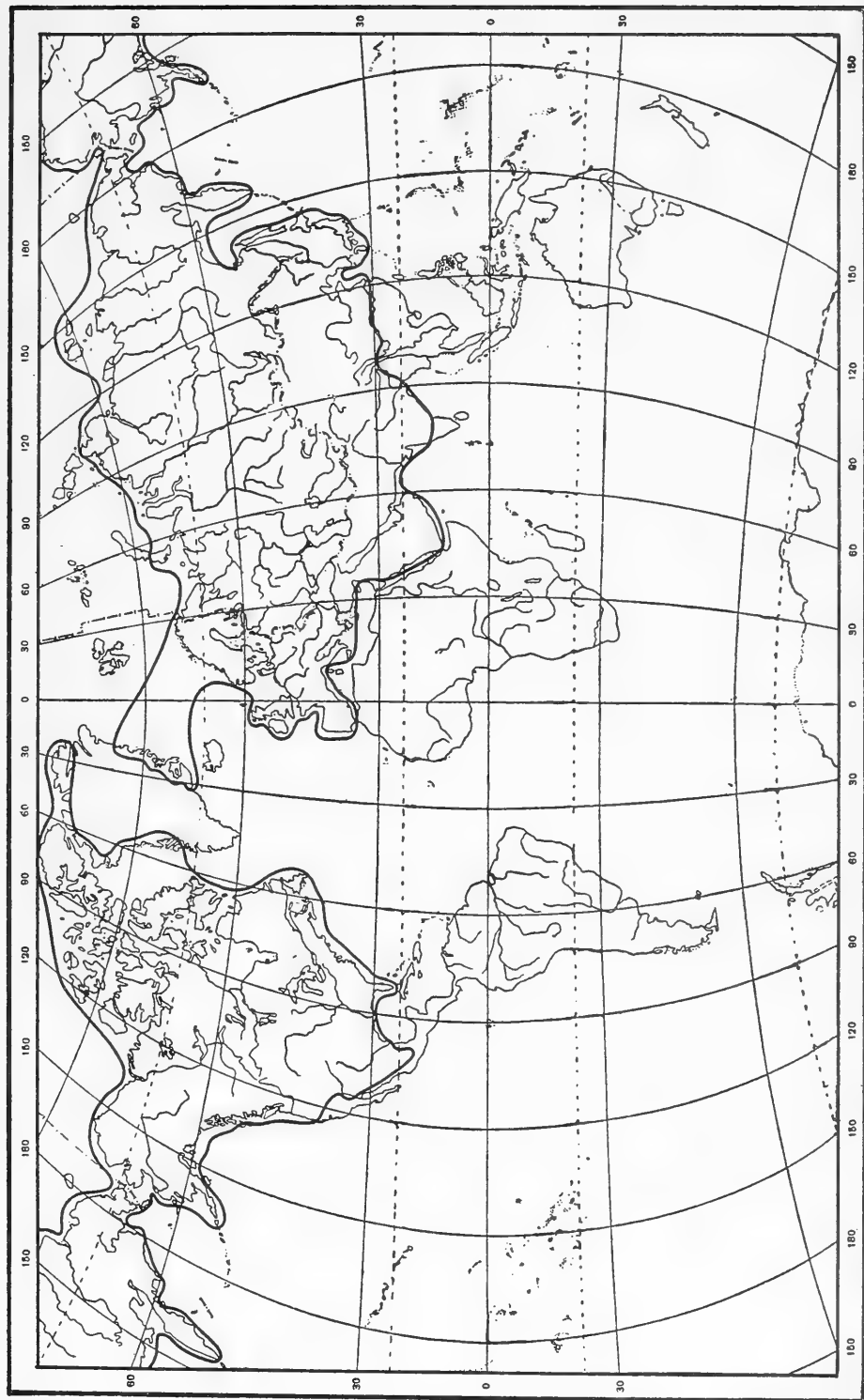


Fig. 51. Reconstructed species range of the wolf, *Canis lupus* L. (V.G. Heptner).

Geographic Variation

The huge range and their occurrence in quite different natural conditions permit us to infer that wolves show considerable geographic variation. Authors of the past century have pointed out the formation of races in wolves. This is confirmed in our own time by many data. However, geographic variation of the wolf is, so far, not satisfactorily studied. This applies to the Old World as well as the New where, in particular, many improbable subspecies were distinguished. However, analyses of several of our populations were made at a good level in recent years. These analyses are, however, very few and concerned only with craniology. Individual variation in color is quite great, and wolf skins are scarce in museums because of their high price. Therefore, one may attempt to characterize at the present moment only a few, better distinguished races of our fauna, and refer only to what may be outlined. This review of the forms and characters given below thus bears a preliminary character.

1. Tundra wolf, *C. l. albus* Kerr, 1798 (Syn. *turuchanensis*, *kamtschaticus*, *dybowskii*).

A wolf of large size. Body length of males (23) 118–137 cm, tail length 42–52; average weight 40 kg, maximum 49 (1 specimen of 55, with the stomach contents). Body length of female wolves (23) is 112–136 cm, tail length 41–49 cm, average weight 36.6 kg, maximum 41 kg.

Greatest length of skull of males (10) 248.5–(M 257.2)–270 mm; females 237.5–(M 247.9 mm)–256.4 mm.

Pelage is very long, dense, fluffy and soft. Length of top hairs is 150–160 mm, guard hairs, 80–150 and underfur, about 70. The usual color is very light and gray; underfur has two zones of color: the lower is lead-gray, the upper is reddish-gray.

Concerning the general light color tone, two main types are found, connected by intermediate forms: light-gray with reddish shade and bluish-gray without this shade. The latter is characteristic of juvenile wolves; old animals are lighter in color and have a reddish frosting. Moreover, the color of the skin changes noticeably during the course of the winter. In November–December, wolves as a group are darker than in April–May, when the fur strongly fades under the influence of the spring sun. Very light individual wolves are sometimes found in May.

Dimensions and color description apply to wolves of Malozemel'sk and Bol'shezemel'sk tundras (Nenets Nats. Okrug, Arkhangel'sk district; Makridin, 1959).

Dimensions of adult Taimyr wolves (caught in 1961) are as follows. Body length of males (11), 123–(M 127.7)–146 cm; of females, 112–(M 121.3)–129 cm; tail length of males, 42–(M 44.4)–48 cm, of
 137 females, 40–(M 42.6)–45 cm; hind foot length of males, 25–(M 26.0)–29 cm, of females, 23–(M 25)–27 cm; ear height of males, 11–(M 12.7)–13 cm, of females, 11–(M 12)–13 cm.

Greatest length of skull of males (6), 258.0–(M 267.0)–288.3 mm, of females (7), 239.4–(M 251.6)–261.4 mm; condylobasal length of skull of males, 238.0–(M 247.6 mm)–*, of females, 221.6–(M 232.3)–243.0 mm; zygomatic breadth of males, 134.3–(M 146.9)–160.7 mm, of females, 132.5–(M 137.1)–142.2 mm; breadth above canines of males, 47.0–(M 51.1)–55.4 mm, of females, 41.4–(M 45.7)–47.3 mm.

Data on maximum weight of northern wolves were obtained from nearly 500 animals caught during 1951–1961, on the Taimyr and westward to Kanin. The greatest weight was of an old male killed on the Taimyr at the mouth of the Dudypa river—52 kg. Two animals, killed on the tundra east of Kanin and on the Yamal, had weights of 48.8 and 46.7 kg (without stomach contents) (V. Makridin).

Found in the tundra zone and the forest tundra of the European and Asian parts of the USSR and in Kamchatka.

Outside the boundaries of the USSR, perhaps in the extreme north of the Scandinavian peninsula.

The belief that the wolves of the extreme north (tundra wolves) are the largest race of Old World and are larger than the forest wolves is quite widespread. Actually, tundra wolves are, apparently somewhat smaller than forest wolves (Makridin, 1959 and others). Statements that in tundra wolves “weight reaches 70 kg and sometimes more” (Kuznetsov, 1952) as a characteristic feature of the population and the subspecies is exaggerated. However, among tundra wolves, specimens of more than 50 kg in weight are found. Moreover, it is possible that the figures given are somewhat reduced, as they were obtained in a locality where intensive hunting of wolves was carried out over the course of several years by aircraft (see later).

As a whole, the tundra wolf is a well-characterized form, and noticeably differs from the forms distributed in the forest zone by its color and, apparently, its dimensions. At present it is impossible to judge whether the wolves in all the area of its distribution are identical or not. Concerning color, wolves of the northern Kola Peninsula are on

*Translator's remark: a figure is missing in original Russian.

the whole somewhat different, and are more similar to forest wolves and wolves of extreme northeastern Siberia. It is not excluded that there are also some differences in the average measurements of the various tundra populations. They have not been studied, but they do not, apparently, exceed the limits of local populations within the boundaries of the subspecies. In the Old World there are no populations of almost pure white wolves similar to those living in the extreme north of America (*C. l. bernardi*, *C. l. manningi* and others of the *tundrarum* group).

This subspecies coincides with the polar assemblage of fur-bearing animals (see beyond).

2. Middle Russian forest wolf, *C. l. lupus* Linnaeus, 1758 (syn. *communis*).

A wolf of very large dimensions, probably maximum within the boundaries of our country.

Color of wolves of this race corresponds to that given above in "Description" (p. 166).

Found in the forest zone of the European part of the country, northward to the northern limit of forest, and southward including the forest steppe. The exact limits of distribution to the south are not known at all; to the west it is to the state boundary and the distribution in the east is not established. It probably spreads more or less far into Siberia, and possibly, occupies western Siberia.

Outside the USSR—in Europe except, evidently, the extreme south.

The Middle Russian forest wolf is well differentiated from the tundra wolf, although in the north, both forms penetrate into the area of occurrence of each other (see "Geographic Distribution").

It is usually considered that the weight of adult males is 40–45 kg, a yearling, about 35 kg and juveniles about 25 kg. Maximum weight of the Middle Russian wolf is considered to be from 69 to 80 kg (see above).

138 Dimensions of animals from separate regions are as follows: weight of adult wolves of northern part of Ryazansk district (south of Meshchera—a little south of the latitude of the Pra river) varies from 32 to 55 kg (based on 173 individuals); weight of the largest male was 56.3 kg (Kozlov, 1955).

Of 65 wolves killed in the region of Mordovsk preserve (Temnikov), only one old male with worn teeth weighed 49 kg. The remaining adult males had weights from 40 to 45 kg; adult females, from 30 to 35 and only one female weighed 38 kg (Kozhevnikov, 1953).

The wolves of Voronezh district, i.e. the forest steppe zone, apparently are somewhat different from Moscow wolves of the true forest zone and have the following measurements and weight. Average body length, based on 154 animals killed in the region of Voronezh preserve, was 125 cm in males and 122 cm in females. The majority of animals, both old as well as yearlings, had a weight from 30 to 40 kg. Many juvenile wolves reached a weight of 23 kg by the end of November. Weight of adult (full-grown) males (48) averaged 40.0 kg; weight of adult (full-grown) females (31) was 31–42.1 kg, averaging 36.0 kg. Weight of yearling male wolves (up to two years old) (8) was 26.6–34.0 kg, averaging 32.0; weight of yearling female wolves (24) was 23.0–32.8 kg, averaging 29.0 kg (weight without stomach contents; Merts, 1953).

Body weight of juvenile and yearling males in Belovezhsk Forest varies from 23 to 35 kg; of females—from 22 to 29 kg (Table 9*).

The described race is related to the largest ones and, probably it, 139 and not the tundra wolf *C. l. albus*, is the largest form of Old World. Beyond that, the figures given show that the average measurements of the Middle Russian “forest wolf”, usually obtained from especially large animals, are often exaggerated. Thus, out of more than 500 accurately weighed animals, only 3 males had a weight exceeding 50 kg, one of these from the Oksk preserve at 56.5 kg (V.V. Kozlov).

Within the defined region, wolves are not entirely of one type. Thus, animals from the extreme west (Belovezhsk Forest) are, as shown, somewhat smaller than from Moscow and, in general, those of the districts around Moscow, but they do not differ in color. Wolves of

Table 9. Dimensions and weight (without stomach content) of adult wolves of Belovezhsk Forest (Gavrin and Donaurov, 1954)¹²

Measurements	Males (about 62 specimens)			Females (about 58 specimens)		
	min.	max.	average	min.	max.	average
Body length	105.0	140.0	119.0	97.0	124.0	111.0
Tail length	33.0	50.0	41.0	29.0	45.0	40.0
Hind foot length	20.0	28.0	25.0	21.0	26.0	23.0
Ear height	11.0	19.0	13.0	11.0	12.0	13.0
Weight	23.3	44.8	34.8	21.0	36.0	29.2

*In Russian original, 10, an error—Sci. Ed.

¹²The authors did not give the number of males and females of their series. The figures given here are based on the authors' indication of sex ratio in the population they studied.

Table 10. Skull measurements of adult wolves of Belovezhsk Forest

Data	Males				Females			
	n	min.	max.	average	n	min	max.	average
Greatest length of skull	41	229.0	275.0	256.5	35	215.0	263.0	224.0
Condylbasal length of skull	35	218.0	253.0	237.1	32	207.0	242.0	227.0
Length of upper tooththrow with canine	43	96.4	117.0	104.9	39	86.8	117.5	99.0
Length of suture between nasal bones	42	72.0	95.0	83.4	40	69.5	90.2	74.7
Interorbital breadth of skull	42	38.4	51.8	45.9	39	33.3	50.8	44.3
Breadth at supraorbital processes	40	48.0	76.4	62.9	36	53.0	72.0	61.2
Breadth behind supraorbital processes	39	37.7	46.7	42.4	36	38.6	47.0	42.3
Zygomatic breadth	40	119.9	153.0	138.9	35	109.0	142.0	131.9

Voronezh district are, apparently, not smaller than those of the more northern districts, although they are somewhat grayer and lighter in color than those of Moscow, the color of which is more reddish. Among 145 winter skins (mainly from Voronezh preserve) 79% were gray, 10% light-gray and only about 20% consisted of skins that had "rusty and bright-rusty" tone (Merts, 1953). It is probable that the lighter color is generally characteristic of wolves of the forest-steppe region. This may be the so-called "Central steppe wolf" of furriers (see beyond p. 195). The Mordovsk wolves correspond to the Moscow ones in color and measurements. Difference in measurements in the relatively small areas mentioned may not represent geographic variation: in places where hunting is very intensive, wolves have little possibility of living to full development and attaining maximum size, and the proportion of the relatively young animals in the population is large.

No comparison was made between our wolves and Scandinavian. However, judging by the characters of animals from our northwest, their assignment to the nominal form is correct.

3. Siberian forest wolf, *C. l. altaicus* Noak, 1911.

A large wolf, not less in size than the Middle Russian, *C. l. lupus*.

Coloration is light gray, darkened along the middle of the back by dark guard hairs. Yellow (ocherous) tones in skin color are absent or weakly developed. The fur is dense, long and soft, but it is slightly shorter and not so silky as that of the tundra wolf. Length of guard hairs on the withers is 9–11 cm.

Found in Siberia and the Far East except the tundra zone, Kamchatka, Trans-Baikaliya and Ussuri territory, and also, probably, the western parts of Siberia; northern Kazakhstan.

Outside the USSR, found in the northern montane taiga of the Mongolian People's Republic.

The systematics of Siberian wolves is not worked out at all, although wolves in the great territory extending from Urals to the Pacific Ocean and from the tundra to the southern mountain ranges are hardly identical. According to one view, the area eastward to Lake Baikal is inhabited by the nominal form distributed in the European part of the Soviet Union (Flerov, 1935), and according to another (Kuznetsov, 1952), it is the "Siberian forest wolf" which is a form different from the Middle Russian and occupying all of Siberia except its tundra parts, and northern Kazakhstan.

Until clarification of geographic variation in Siberian wolves, this form is conditionally separated. The name given here is also condi-

tional, it being, apparently, the only one applicable to the Siberian forest wolf. Since the western Siberian and northern Kazakhstan wolves are, apparently, very close to the Middle Russian ones, then the name *C. l. altaicus* is, above all, applied to the Middle- and East Siberian animals.

4. Steppe wolf, *C. l. campestris* Dwigubski, 1804 (syn. *arundinaceus*).

Average dimensions are somewhat less than the Middle Russian wolf, *C. l. lupus*. Pelage is shorter, coarser and sparser. Color of the sides is relatively light, gray, on the back rusty-gray or brownish with a quite strong admixture of black hairs.

140 Found in the Pri-Caspian steppes, steppes of the Cis-Caucasus and the lower Volga, the steppes of Kazakhstan (except the north?), and the steppe region of the European part of the Union.

Outside the USSR, perhaps in the steppe section of Romania and Hungary (in the past).

Apparently, this is the wolf of the Kazakhstan steppes (except the north), intermediate between the northern forest and southern desert wolves, which also penetrates into the steppes of the Cis-Caucasus and the European part of the Soviet Union. However, it is a form of weakly determined characters and distribution. The differences between steppe wolves and Middle Russian ones have been mentioned and are accepted by all authors, and they obviously exist, although there has been no study of this question based upon reliable material. At the present time, the wolf is absent or very rare in considerable areas of our European steppes. In the northern Ukraine and to the west, also in the steppe lives, apparently, not the true, relatively small, steppe wolf, but the larger forest or "forest-steppe" form. It is probable that the latter colonized the western parts (Odessa, Khersonsk, Nikolaevsk districts), where the true steppe wolf was almost completely exterminated during war and in the post-war years (Korneev, 1950).

In the population of steppe wolves, particularly in the Ukraine, few very large individuals are encountered (see above). They are mainly found in the northern part of the steppe zone. Apparently, these individuals intrude from the north (see beyond).

C. l. campestris, apparently, corresponds to the "Caucasian steppe wolf" (see later).¹³

¹³In recent years, many references deal with the problem concerning the existence in the past in the steppes of Hungary of the very small "reed wolf", sharply distinguishable from the large Carpathian forest wolf. According to the view of some

Note: With regard to the type locality selected here (Cis-Caucasian steppes) (see synonymy), the following must be taken into consideration. Dwigubsky states "in desertis ad mare Nigrum et Caspium interjacentibus, Kirgisicis, Bucharicis, ad f. Yeniseam, ubi, dantur colore sordide flavorubentes" (1804), i.e. "In desert places situated between the Black and Caspian seas, in Kirgiz steppes, in Bukhara, and at the Yenisei river where dirty-yellowish-reddish forms are encountered", or "in the steppes near the Caspian and Black seas; in Kirgiz steppes and near the Yenisei river, where red wolves also occur" (1830).

In all the districts outlined by Dwigubsky, wolves are undoubtedly not identical. In accordance with the beginning of the first text given, and in connection with the unclear systematic position of wolves in the west of our steppes (Ukraine), it is here suggested to restrict the very wide definition of Dwigubsky to the mentioned *terra typica restricta*. Dwigubsky [Dvigubskii] moreover stated (1830) that "in my traveling in the steppe between the Dnepr and the Don, in 1805 (i.e. after the publication of the description. V.H.), I had occasion to see such wolves even in the Bakhmuts'k district near the Donets."

The suggestion about the affiliation of the name *campestris* to the jackal (Pocock, 1941) has no scientific basis; in almost all the territory mentioned by Dwigubsky, the jackal is absent and was never previously found.

5. Caucasian wolf, *C. l. cubanensis* Ognev, 1922 (syn. *hajaestanicus*).

Wolf of medium dimensions (less than Middle Russian). Winter coat is poorly furred, coarse, short and quite sparse. Length of guard hairs on the withers does not usually exceed 70–75 mm. Coloration is dirty, dull gray-ocherous, quite dark due to the more or less evenly distributed guard hairs on the skin. Greatest length of skull of males 240–272 mm, of females 224–251 mm; condylobasal length of skull of males is 221–250 mm, of females 209–234 mm; zygomatic breadth of skull of males 128–152 mm, of females 11*–132 mm.

Found in the Great Caucasus and Trans-Caucasus.

Outside the USSR it is not known; probably spreads into the contiguous territories of Iran and Turkey.

authors, which is, apparently, justified, the "reed wolf" is simply the jackal. It is not excluded that our steppe wolf described above might have penetrated quite deeply to the west. It is not, however, similar to that described by some authors (Nad) under the name "reed wolf" (Rohrwolf).

*Error in original Russian text—Sci. Ed.

- 141 The distinctiveness of Caucasian wolves is mentioned by a series of authors and is, evidently, real. However, the form is very poorly studied. Its distribution is also little known. Moreover, in various parts of Caucasus, wolves are, apparently, not identical. Thus, on the plains of the Trans-Caucasus, the animals are somewhat smaller than those inhabiting the northern Caucasus. It is possible that small animals belonging to the group of desert wolves (*desertorum-pallipes*), described from Asia Minor, penetrate here from the south. Wolves of the Armenian highlands, described as *C. l. hajastanicus*, are somewhat larger than those of the plains (they correspond, in dimensions, to those inhabiting the Kuban Caucasus) and have softer, longer fur (Dal', 1951; Vereshchagin, 1959). However, their separation as an independent form is insufficiently argued.

6. Desert wolf, *C. l. desertorum* Bogdanov, 1882 (syn. *bactrianus*).

Measurements are considerably less than those of northern forest wolves; the smallest form of those inhabiting our country.

Coloration is light, gray-sandy or yellowish-gray with a few black guard hairs on the upper part of the body, mainly along the spine. In the area of the occiput and the outer side of the ears, reddish tones are developed. Winter fur is not very luxuriant; quite sparse and coarse. The tail is poorly furred.

Weight reaches 35–40 kg.

Found in plains areas, including the deserts of Middle Asia and southern Kazakhstan north to the middle Emba, and the northern Pri-Urals and in the northeast to the region of the Chuya river, Betpak-Dala and Pribalkhash'e.

Outside the USSR, found in Afghanistan and Iran, at least in the northern parts of these countries.

The desert wolf represents a well-differentiated form. Specific, precise data on the dimensions of this form have not been published, although its small measurements are indicated by all authors. At the same time, large individual specimens are encountered in the wolf population of Turkmeniya (Heptner, 1956).

The wolf of the Trans-Caucasian plains and the Mongolian Republic has much in common with the desert one. *C. l. desertorum* is, evidently, closely related to the Indian wolf, *C. l. pallipes*, although this form is, apparently, still smaller and also somewhat differentiated by coloration and in fur characteristics. The boundary between the geographic ranges of the forms *desertorum* and *pallipes* is unknown.

This form, apparently, corresponds to "Middle Asian steppe wolf" of the Middle Asian bloc of furriers (see beyond).

7. Tibetan wolf, *C. l. chanko* Gray, 1863 (syn. *laniger* auct., nec *laniger* Smith).

Dimensions comparatively small, noticeably smaller than *C. l. lupus*, but slightly larger than *C. l. desertorum*.

The coloration is light, whitish-gray with an admixture of darker brownish tones on the upper part of the body. Along the spine there is a well-defined dark stripe. The winter fur is soft, long, quite luxuriant, with a well-developed undercoat. The tail is densely furred with long hairs.

Weight, apparently, does not exceed 45 kg.

Found in the Pamirs proper and the Pamir-Alai system and also the Tien Shan.

Outside the USSR, it is found in montane regions of Central Asia, Dzhungariya and Tien Shan, across Tibet to Gansu, Sichuan and Yunnan in the east and Inner Mongolia in the north.

This well-defined race corresponds to the "forest (mountain) wolf" of the Middle Asian fur trade.

Note: As regards the name and type locality of this form (see synonymy) the following must be taken into consideration. "Chinese Tatar," from which it was described, is extremely ill-defined. However, none of the authors concerned with the nomenclature of wolves (Allen, 1938; Pocock, 1941) attempted to specify it. This form has been given a very wide distribution in Central Asia "from Chinese Turkestan and the Tien Shan through Tibet into Mongolia, northern China, Shanxi, 142 Sichuan, and apparently, Yunnan; the western Himalayas in Kashmir, at least from Chitral to Lahul" (Pocock, 1941). The uniformity of wolves in these regions and above all the identity of the animal of the low desert of Kashgariya (Chinese Turkestan) and high montane Tibet and the Himalayas is very doubtful. Since the long furred wolf is, first of all, associated with Tibet, and since the name *chanco* is employed in place of the name *laniger* to Tibet animals, it is here suggested that the *terra typica* of the form *chanco* be considered Tibet.

Within the borders of the Kazakh republic, therefore, the ranges of four races of wolf come together. In the north (still 100–130 km south of Kustanai, V.G. Heptner) and in the extreme east, the large "Siberian [and Middle Russian] forest wolves" (*C. l. lupus* and *C. l. altaicus*) live. In the south is distributed the small, sandy-colored desert wolf, *C. l. desertorum*. The entire intervening region is, apparently, occupied by

a form transitional (intermediate) between them. It evidently follows that it should be considered *C. l. campestris*, the range of which passed through the region north of the Caspian Sea westward to the southern Russian steppes. In the steppes of Kazakhstan, far beyond the region of its usual occurrence, isolated individuals of both the southern and, especially the northern forms, wander. Wolves of the northern type have been noted at middle Emba (Afanas'ev et al., 1953). In Tien Shan the montane form, *C. l. chanco* lives. There is insufficient basis to assume the existence in Kazakhstan of two undescribed subspecies (Afanas'ev et al., 1953).

8. Mongolian wolf, *C. l. tschiliensis* Matschie, 1967 (syn. *argunensis*, *dorogostaiskii*).

Dimensions are not large—like *C. l. desertorum*, or somewhat larger, but markedly smaller than those of the Siberian forest wolves.

Coloration is dirty gray, frosted with a weak admixture of ochereous color and without bright pale-yellow and chestnut tones. The fur is coarse and stiff.¹⁴

Total body length of males (18), 93–(M 115)–158 cm; tail length, 30–40 cm; hind foot length, 16–24 cm; ear height, 10–14.5 cm; shoulder height, 58–89 cm. Weight, 26–(M 31.3)–37 kg. Total length of females (8), 90–(M 99.6)–109 cm; tail length, 30–40 cm; hind foot length, 16–23 cm; ear height 9.5–13 cm; shoulder height, 57–75 cm. Weight, 22–(M 27.7)–30 kg (animals from southern part of Ussuri territory; G.F. Bromlei).

Greatest length of skull of males (5), 226.0–(M 2393.7)–253.5; condylobasal length of skull (3), 224.0–(M 229.8)–236.5; interorbital breadth (5), 38.5–(M 42.0)–45.5; postorbital breadth (5), 38.5–(M 40.5)–43.5; zygomatic breadth, (5) 114.0–(M 126.7)–139.5 (specimens from eastern Trans-Baikaliya; Skalon, 1936).

Found in eastern, southern and southwestern Trans-Baikaliya and in the Ussuri territory.

Outside the USSR, in the Mongolian Republic, except the northern montane and taiga parts, in Inner Mongolia and probably, on the Korean peninsula.

The described form is, apparently, quite well characterized—it is the wolf of the eastern (Central Asian) section of the steppe and desert

¹⁴Statements that the "eastern (Trans-Baikal) wolves differ by their long tails, in the majority of cases curved upwards at the end" (Manteifel' and Larin, 1949) cannot be considered seriously.

zone of Eurasia. Based on its coloration and dimensions, it possesses features relating it to *C. l. desertorum*. Generally, this form is still very poorly studied. (Characteristics and distribution based on data of Skalon, 1936; Loukashkin and Jernakov, 1934; and G.F. Bromlei.)

Within the USSR, apparently only a narrow strip of the northern edge of its range is found; the Siberian forest wolf lives around Lake Baikal and, probably, around Chita.

The presence of this "steppe" form in the forests of Ussuri territory is related to wolves from the south having reached there only in the present century in connection with the clearing of taiga and the decrease in the number of their antagonist—the tiger. Formerly, wolves were generally absent.

143 The nomenclature of this form is unclear. The name employed, given all the inadequacies of description is, apparently, concerned with it. At present there is no basis for suggesting that the wolves of Trans-Baikaliya and northeastern China differ from those from Liaodun*. Nevertheless, the name *tshiliensis* is considered conditional pending a solid systematic revision of the wolves of Inner Asia and the Far East.

9.? Sakhalin wolf, *C. l. hattai* Kishida, 1931 (syn. *rex*).

The characteristics of this proposed form are unclear and its independence cannot be considered established. Its description is unsatisfactory. It was described from Hokkaido, where it is now exterminated. It was applied to Sakhalin and "perhaps" to the Kuril islands (Harper, 1945; Ellerman and Morrison-Scott, 1951). As shown above (see "Geographic Distribution"), the wolf is absent on the Kuril chain, and on Sakhalin, it has not been met with since the beginning of the present century. Therefore, it is impossible now to decide which wolf lived on Sakhalin. Intrusions of the Siberian forest wolf occur from the mainland across Nevel'sk Strait on the ice but, apparently, it does not remain.

* * *

Geographic variation in the wolf finds its reflection in the sorting of skins into groups, as is usual in the fur trade and this attracted the attention of zoologists. The value of these data lies in the fact that they are based on the examination of large quantities—tens of thousands of skins. In some cases, there is a quite exact coincidence of the groups with subspecies, while in others, differences in classification are substantial.

*Place in northeastern Xinjiang province—Sci. Ed.

“Characteristics of winter-killed skins of different groups of wolves are as follows:

Polar group: The entire tundra and forest-tundra belt of the USSR and Kamchatka.

Skin size is very great. In spite of the thin flesh side of the skin, large size of skins gives them a considerable weight—one hundred skins weigh on average 150 kg. Weight of adult animal reaches 70 kg, and sometimes more. Pelage is especially luxuriant, thick, and in particular, very soft. Length of guard hairs on the nape of winter skin is 11–13 cm. The abdomen is covered with long dense fur. The flesh side of the hide is light and thin. Coloration of the fur is light or dark gray, tinged with bluish. Wolves of the Siberian tundra have usually the spine and the sides of light, pale-grayish color tinged with blue. The dark guard hairs grow mainly on the spine, forming a longitudinal belt; on the sides, dark tips of the guard hairs are not well defined. The abdomen and lower thorax are whitish. The limbs are almost white.

In the extreme north of the Far East, wolves have similar color but usually mixed with a yellowish tinge. Murmansk wolves have a darker color due to the great development and distribution of black tips of the guard hairs on the skin.

Siberian group: All of Siberia and the Far East except the tundra regions, and also the northern part of Kazakhstan.

The group is subdivided into skins of the Siberian forest and steppe wolf.¹⁵

144 *Siberian Forest wolf*. Skins have the same measurements as those of the polar wolf. Weight of one hundred hides is 148 kg. Weight of an adult Siberian wolf reaches 70 kg and even more. Pelage is dense, long and soft, but is of lower quality and not so silky as that of the polar wolf. Length of guard hairs on the nape ranges from 9 to 11 cm. Flesh side of the skin is compact and quite thick. Coloration of winter fur is usually light gray, darkened along the spine due to dark tips of the guard hairs. Yellow tints are either absent or poorly developed. Abdomen is whitish. Limbs are gray.

¹⁵Division of the group into subgroups of forests and steppe generally reflects the basic types of individual variation in coloration and fur quality. In some cases it indicates the migrations (sometimes seasonal) of a certain number of animals of one race into a region inhabited by another race. Sometimes, as mentioned above, these groups correspond to particular subspecies.

Data on animal weight, as mentioned above, in the reviewed groups is sometimes overstated.

Siberian Steppe wolf. Skin size is as in the forest wolf. Pelage is moderately luxuriant, but coarse. Coloration of the spine and the sides is gray with clear brownish or reddish tints and with black tips of the guard hairs on the spine well developed. Abdomen is reddish or yellowish. Limbs are brown.

Kazakhstan group: Kazakhstan, except its northern regions.

Skins of the Kazakhstan group are also divided into skins of the forest and steppe wolf, which are similar to the hides of steppe and forest varieties of the Siberian wolf, but differ in their smaller dimensions and less luxuriant pelage (weight of 100 hides of Kazakhstan wolf is 112 kg, and length of guard hairs on the withers of forest wolf reaches 7 cm).

Middle Asian group: Middle Asia.

Skins of this group are divided into skins of forest (more correctly, montane) and steppe Middle Asian wolves.

Forest (montane) Middle Asian wolf. Dimensions are small, and weight of 100 hides is not more than 100 kg. Weight of an adult animal does not exceed 45 kg. Pelage is quite soft and long, but not particularly dense. Coloration is light-whitish-gray, slightly darkened on the spine by dark guard hairs. Side and abdomen are whitish.

Steppe Middle Asian wolf. Dimensions are still less than montane wolves of Middle Asia. Live weight is usually less than 40 kg. Pelage is not very luxuriant, coarse, coloration of spine is light yellowish-gray. Abdomen is grayish.

Central (Russian) group: European part of the USSR, except tundra regions, Ukraine, Crimea, northern Caucasus, and the lower Volga area. They are divided into the forest and steppe central wolves.

Central forest wolf. Dimensions are large—nearly the same as those of the Siberian forest wolf. Weight of 100 hides is 166 kg. Weight of live animal is up to 70 kg. Pelage is of average luxuriance and softness. Length of guard hairs on the withers is usually not more than 9 cm. Coloration of fur in the majority of skins is quite dark, gray, usually with brownish tints. The quite dark color of the skin is due to there being black guard hairs distributed on the entire middle dorsal part of the skin, somewhat darker in the region of the vertebrae. Abdomen is whitish or yellowish.

Central steppe wolf. Dimensions are slightly less than the forest form. Pelage is not very luxuriant, coarse and bristly. Coloration of the spine and sides is brownish or reddish-gray. Abdomen is yellowish.

Caucasian group: Ukraine, Crimea, northern Caucasus, Trans-Caucasus, lower Volga area.

Skins of this group are subdivided into two categories: forest and steppe Caucasian wolves.

Caucasian forest wolf (true montane. V.H.). Dimensions moderate. Weight of 100 skins is 146 kg. Weight of live animal reaches 50 kg. Pelage is not very luxuriant; sparse, coarse. Length of guard hairs on the nape is not more than 7.5 cm. Flesh side of the skin is porous and thick. Coloration of the spine and the sides is dirty-gray, usually quite dark due to numerous evenly distributed dark guard hairs. Abdomen is dirty whitish with yellow tints.

Caucasian steppe wolf. Dimensions are the same as those of the forest wolf. Pelage is short, sparse, and coarse. Flesh side of the skin is thick, porous. Coloration of the spine is usually rusty-brownish or
145 rusty-gray with dirty tints, and is strongly darkened from dark tips of the guard hairs. Sides are lighter in color. Abdomen is dirty-whitish.

Skins of the polar wolf are considered the most valuable—among the remaining, the best are skins of the Siberian wolf; skins of the Central and Kazakhstan wolves are less valued, and those of Middle Asian wolves still less so; the poorest skins are those of Caucasian wolves” (Kuznetsov, 1952).

* * *

From parts of the range lying outside the boundaries of our country in the Old World, the following forms are recorded.

1) *C. l. signatus* Cabrera, 1907—Iberian Peninsula; 2) *C. l. deitanus* Cabrera, 1907—Spain; 3) *C. l. italicus* Altob., 1921—Italy and Sicily; 4) *C. l. kurjak* Bol'kay, 1925—Yugoslavia; 5) *C. l. hodophylax* Tamm., 1839—Honshu, Hondo*, exterminated; 6) *C. l. pallipes* Sykes, 1831—India, Baluchistan, southern Iran, Iraq, ? Asia Minor, northern part of the Arabian peninsula; 7) *C. l. arabs* Pocock, 1934—southern part of the Arabian peninsula.

The existence of some forms in Europe (two in the Iberian Peninsula) is very doubtful, the remainder are, apparently, real (especially *C. l. pallipes*).

*Honshu and Hondo are synonyms, the first being the modern, the second the old, name of the main Japanese island—Sci. Ed.

Geographic variation of wolves in the Old World, as regards characteristics of size and also color is quite regular. The largest wolves are northern, in the tundra and forest zones.

Steppe wolves are somewhat smaller in size, as in wolves of the Caucasus, and wolves of the deserts of Middle and Central Asia are still smaller. Wolves of this type also inhabit the mountains of Central Asia; if some of them are larger than those of desert plains, the difference on the average is usually insignificant. The smallest wolves inhabit the southern margins of the range—India, Baluchistan, Iraq and the Arabian peninsula¹⁶. Wolves of types *desertorum*, *tschiliensis* and *chanco* comprise a transitional group from the large northern to the small southern ones. Accordingly, Bergman's rule is quite clearly demonstrated.

Wolves with the lightest color are those of the extreme north—the tundra zone; more southerly ones living in the forest zone are more intensely colored, while those of the extreme south—the desert zone, have light ochreous “desert” color. Animals of the mountains of Central Asia are somewhat more intensely colored than in the desert. Accordingly, Gloger's law is also demonstrated.

Geographic variation in New World wolves is well demonstrated. Twenty-six well-founded forms are usually accepted (Young and Goldman, 1944; Miller and Kellog, 1955; Haltenorth and Trense, 1956; Hall and Kelson, 1959)¹⁷. Both *a priori* and from the published materials, it is sufficiently clear that this number is overestimated and the number of actually existing and the really differentiated subspecies of American wolves is considerably less. Nevertheless, there is no doubt that geographic variation of animals on this continent is clearly expressed and significant. There is a quite definite geographical trend related both to size and color.

The largest wolves live in the North; towards the south they gradually become smaller, having minimal dimensions in the south of the range. The largest wolves are in the extreme northwest—in Alaska and the Mackenzie basin (*pambasileus*, *mackenzii*, *tundrarum*). Here animals attain a weight of almost 80 kg; the known maximum weight is

¹⁶For the Indian *C. l. pallipes*, Pocock (1941) recorded a maximum body length of 100 cm and greatest weight of 24 kg (53 pounds). Weight is, evidently, sometimes more.

¹⁷Since the complete list of these forms is of limited interest to our readers, it is not given here.

The area of all North America is greater than the territory of USSR by only a little more than 2 million km².

175 pounds—79.3 kg; but on average their weight is less, and 45.4 kg (100 pounds) is the weight of a large animal. The smallest wolves live in the extreme south. Those of Texas and Mexico, *C. l. baileyi*, and still smaller are those inhabiting the extreme southeast, *C. l. rufus*. Weights of the males of this form reach 32–36.5 kg (70–80 pounds), but on average the animal weighs 14–16 kg (30–35 pounds). In this way, the American wolves follow Bergman's rule more clearly and more sharply than do the wolves of the Old World.

Coloration of American wolves also changes geographically in a regular manner. In the extreme north and northwest live the northern tundra wolves. Some races (populations) have a nearly white color (*C. l. manningi*, *C. l. bernardi*, *C. l. tundrarum*). Wolves of the forest zone have a more saturated coloration, which generally corresponds to the coloration of our forest wolves. Steppe, and especially desert forms of the south and southwest have light ochreous tones. In the extreme southeast of the range, in mesic portions of the country, in the area of the lower course of the Mississippi and in Florida, the wolves have a very intense color with well-developed ochreous and red tones ("red wolf" of the Americans). Here, melanists are encountered with greater frequency than in any other place, and the coloration of local animals is generally dimorphic¹⁸. In this way, Gloger's rule is sufficiently clearly revealed in the described color distribution (V.H.).

Biology¹⁹

Population. Within the boundaries of their range, wolves are very unevenly distributed. Their distribution over a territory is conditioned by the abundance and the stability of food resources, primarily wild and domestic ungulates, and by the possibilities of capturing them, which depends in winter on the depth and friability of the snow cover.

¹⁸American authors usually consider the wolves of the southeast as a separate species, *C. niger* Bartram, with three subspecies (*niger*, *gregoryi*, *rufus*). This fact is hardly well founded. Through the small *C. l. lycaon* of the southwest, both groups of races, "*C. lupus*" and "*C. niger*," merge with each other. Here, the forms of the *niger* group are assigned to *C. lupus*.

¹⁹Information on the life habits, distribution and abundance of wolves appears in a large number of journal notes and articles, and separate books, and in faunistic studies and reviews, but only a part of this material represents scientific publications based on original and accurately collected data. Therefore, the ecology of wolf cannot be considered well studied. Information on the biology of individual populations and subspecies is especially scarce.

On the Kola Peninsula, in the second half of the past century, the wolf was very rare, resulting from a decrease in the number of wild reindeers and the reduction of domestic reindeer herds of the Saami (Laplanders). Wolves at that time were relatively numerous along the boundaries with Sweden and Norway, in their eastern regions where the wild reindeer was preserved and where domestic reindeer breeding was in better conditions (Pleske, 1887). In the Lapland preserve, in 1929–1938, wolves were totally absent and it was only later that they began to bother herds of wild reindeer. In the winter of 1940/41, only three wolves lived in the preserve in an area of 1300 kg² (Semenov-Tyan-Shanskii, 1948).

In the Karelian ASSR, they [wolves] continually inhabited the southernmost regions settled by humans. In certain years, wolves were numerous in the Pri-Onega and Olonetsk regions, in Trans-Onega and in those regions of the republic with little forest, especially along the White Sea coast (Stroganov, 1949). The wolf is rare in the Segezhs'k region, and in the northern regions of the Karelian ASSR with deep snow (White Sea, Kemsk and Loukhsk regions), it does not live continuously, appearing periodically every 5–10 years. Their appearance is connected with the driving of domestic reindeer herds or the migration of wild reindeer (Marvin, 1951, 1959).

- In the tundra and forest-tundra of the European part of the USSR, wolves are relatively numerous; they accomplish seasonal migrations, in summer going onto the tundra and in winter, into the forest-tundra.
- 147 In the Mezensk region, wolves are few in summer and numerous in winter, since some of the migrants from the Kanin tundra approach localities of resident wolves. In summer, only a few pairs remain to raise their young on the Koidinsk tundra (Abramovsk coast of Mezensk Gulf) and along the northern tributaries of the Nes'. On the Kanin peninsula, wolves are encountered the year round. By the beginning of winter, the majority of wolves wander into the forest-tundra; some migrate to the Mezensk region, but the main mass winters on the southern coast of Cheshsk Gulf. To this region also come wolves from the Timansk tundra. In summer, not more than 3–4 pairs of wolves remain in the huge area of the Cheshsk Gulf from Nes' village to the lower Pesh (along the Vitasu, Ome, Snope rivers).

On the Timansk and Malozemel'sk tundras, wolves den along the Volong, Travyank, Shchuch'ei, Indige, Belaya, Svetlaya, Kamennaya Visk, Vel't', Nerut, and Sul rivers and their tributaries. On the Timansk and Malozemel'sk tundras, wolves remain in summer in the Timansk range; near the coast, they are exceptionally rare.

On the Bol'shezemel'sk tundra no wolves are found in the reproductive period in a coastal strip about 100 km wide, where there are few suitable den sites, and in summer, herds of domestic deers are pastured along with numerous dogs. Wolves den in the basins of the upper courses of the Shapkinaya, Kuk, Lai and Kolva rivers (western part of Bol'shezemel'sk tundra), along the upper Adz'va, Bol'shaya Rogovaya and Chernaya (central part) rivers, and in the Pai-Khoi range and the upper Korotaika, Silovaya and Kara (eastern part) rivers. In winter, the majority of wolves migrate from the Bol'shezemel'sk tundra to the forest-tundra, from the bend of the Pechora to the upper Usa; some move beyond the Urals (Semenov, 1954).

Wolves are generally fewer on the European tundras than in Arkhangel'sk taiga. On the Timansk tundra only 10 wolves were found in an area of 10 thousand km², or 1 wolf per 1000 km². In autumn, in the event of successful reproduction, the number here could be 2.8 wolves per 1000 km² (Semenov, 1954).

In the taiga forests of Arkhangel'sk district, wolves are common in the southern and central regions—in the basins of the Northern Dvina and Onega. Along the valleys of these rivers, and sometimes of the Pinega, wolves, singly and in groups, traverse northward. In the Priozernii region, from 1947–1952, the number of wolves did not exceed 40–45 individuals in autumn (3 wolves per 1000 km²; Semenov, 1954). In Arkhangel'sk district, the wolf prefers places where the taiga is thinned by cutting, the forests are intersected by roads and close to villages where there are large areas of fields, floodplains and forest cuttings since, in winter, the wolf finds its food only near humans. In other northern districts with developing agriculture, the number of wolves also increases, and the districts inhabited by them spread northward (Semenov, 1954).

In the Komi ASSR, wolves are rare. In the taiga, they are only encountered in the river valleys and lake depressions. They are more common in the agricultural landscapes of the southern subzone of taiga, and on the tundra. During 12.5 years (1939–1950) in the Komi ASSR only 343 wolf skins were tanned. The average number tanned yearly from 100 km² of taiga ranges from 0 to 0.01; in regions with agricultural and other open lands, from 0.01 to 0.06 skins (Ostroumov, 1953).

In the Urals, wolves are most numerous in tundra, forest-steppe and steppe. Their distribution there is also closely related to human settlement. Deep in the taiga, wolves are few or totally absent (Shvarts, Pavlinin and Danilov, 1951).

In Yamalo-Nenetsk Natl. Region, the wolf is met with almost everywhere, but dens mainly in the southern tundra belt, in forest-tundra, and in the thin forest of the pri-tundra. In winter, it remains in the immediate neighborhood of domestic reindeer herds and is, therefore, very rare in the Arctic tundra. In the taiga, it only rarely appears in the Krasnosel'kupsk region and in the southern parts of the Purovsk, Nadym'sk and Shuryshkarsk regions. During a decade (1948–1957), 1166 wolf skins were tanned from this area (85 to 157 per year) (Rakhmanin, 1959).

148 In western Siberia, the number of wolves is high in the southern tundra, in forest-tundra, southern taiga, birch forest-steppe, and steppe. The northern and middle parts of taiga zone are distinguished by low numbers of wolves to the west (the regions to the west of the lower and middle courses of the Irtysh and the lower Ob'). Wolves only traverse the region between the lower Irtysh and middle Ob' in some years. Thus, in the Surgut'sk region, only 2 wolves in all were caught in 20 years, and in Vasyugan', only two intrusions were recorded over 12 years. Breeding by wolves has never been recorded in these regions.

The somewhat unexpected northeastern maximum in wolf numbers in western Siberia originates in the area with maximal depth of snow cover, but this area is notable for its compact snow cover and the abundance of wild and domestic reindeer. In the south, regions with high wolf density coincide with the places of high number of roe deer, regions of developed stock-breeding, and uneven snow cover (Laptev, 1958).

Along the Yenisei, in the taiga zone, the wolf is rare everywhere until Turukhansk. In the forest-tundra (north of 76° N. Lat.), wolf numbers noticeably increase. Places of wolf concentration on the tundras are restricted to the regions of pastures of domestic reindeer herds or stopping places of wild ones (S. Naumov, 1931). Wolves are common on the Yenisei delta; periodically they are very abundant along the lower Olenek, Yana and Lena [rivers]. In central and southern Yakutiya, wolves are few, but in Verkhoyansk territory there are more, and in the Kolyma and Chukotsk lands, they are relatively numerous. Along the Anadyr, they are common (Ognev, 1926; Sikol'nikov, 1928). In the Lyakhovsk islands the wolf, being closely associated with tundra and reindeer, is encountered only in summer and in winter migrates away, following the deer herds to the mainland (Tugarinov, Smirnov and Ivanov, 1934).

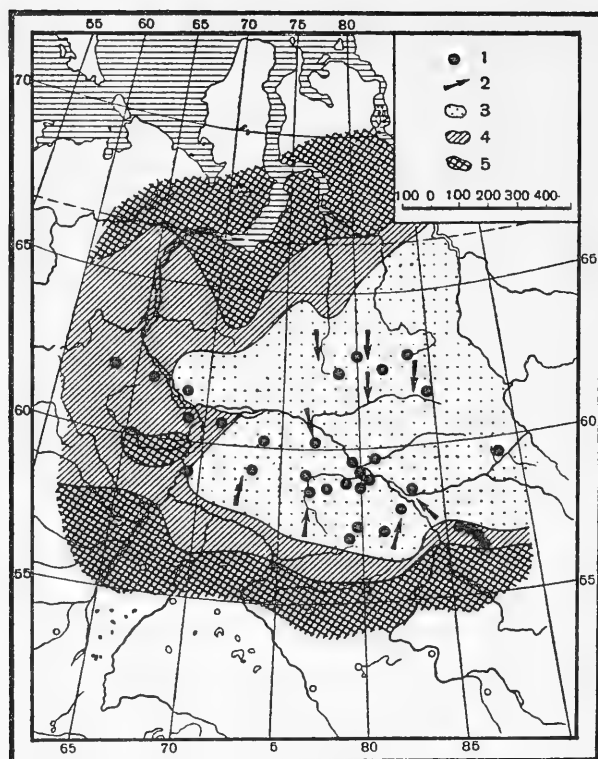


Fig. 52. Distribution and relative numbers of wolves in western Siberia (from Laptev, 1958): 1—individual occurrences, 2—direction of migrations, 3—area of migrations, 4—low population density, 5—high population density.

In the taiga zone of middle Siberia, in the Nizhnaya and Podkamennaya Tunguska basins, wolves are most numerous in the upper Khatanga-Kotui, Vilyuyi, Moiero and the northern tributaries of the Nizhnaya Tunguska, where large herds of domestic reindeer graze. Along the Podkamennaya Tunguska, to the lower course and southern tributaries of the Nizhnaya Tunguska, wolves are scarce because of deep, porous snow cover and the small number of wild and domestic ungulates. Wolves usually appear here only for a short time (N. Naumov, 1934). This area of low numbers and nonpermanent habitation of wolves
 149 on the right bank of the Yenisei almost joins with a like minimum in wolf numbers in western Siberia (interfluvies of the Ob', Taz and Yenisei rivers).

In Lena-Khatanga district, wolves are common along the Olenek and along the Muna—a tributary of the Lena. In the Vilyuyi basin the

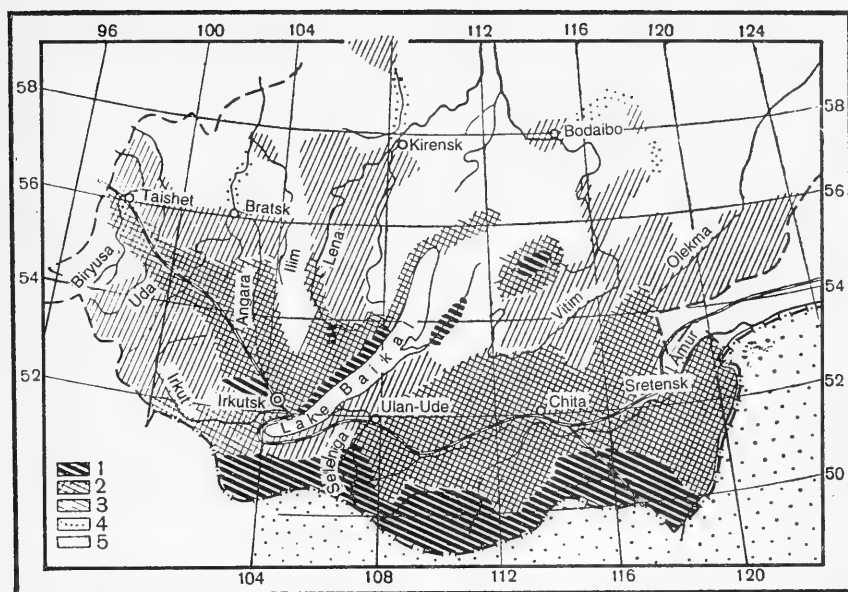


Fig. 53. Distribution and relative numbers of wolves in eastern Siberia (from Khudyakov, 1957): 1—wolves numerous, 2—common, 3—rare, 4—transient, 5—wolves absent.

wolf is rare, and its numbers increase only above the Arctic Circle (along the Olenek). But in the valley of the Vilyuyi itself, they are relatively numerous. In central and southern Yakutiya, and also in the Kolymo-Indigirsk territory, the wolf is rare even in settled regions, or is only found sporadically, but it is common on the tundra and forest-tundra.

In the taiga zone of eastern Siberia, in the Sayans and Altai, the wolf is scarce due to deep snow. These predators appear here only in those regions where domestic or wild ungulates are common and where thinning or reduction* of forests by humans was promoted by reduction in porosity and depth of snow cover. In the Altai and Sayans, wolves are few, and in the majority of regions they only appear accidentally. In the mountains, in autumn, they follow roe deer into the valleys, where the snow is shallower and firmer (Polyakov, 1866; Solov'ev 1921; Afanas'ev et al., 1953).

In eastern Siberia, wolves are very abundant along the border with the Mongolian Republic; in the southern Pri-Baikal, near Irkutsk, they

*Misprint in original Russian; *svedenie* (information) instead of *snizhenie*—Sci. Ed.

are common in regions along the railway (Pri-Baikal, Trans-Baikaliya). The predators are rare or absent in the northern and a bit of the southern taiga in regions of deep snow (Table 11).

In the taiga of the Far East, the wolf is also rare in all regions of deep snow, especially those little opened up by humans. Wolves are common in places with abundant wild or domestic ungulates and in regions where the taiga has been considerably thinned by logging. In Primor'e, the predator is rare—along the Iman (Ussuri territory), they are encountered principally in its lower course (Zolotarev, 1936).

In the middle and southern zones of the European part of the USSR, including the Pri-Baltic, wolves are rare. Their number grew during war time, 1941–1945, but as a result of intensive control, at the present time their numbers are again reduced. In Belorussia, the wolf is met with everywhere. In 1932–1939 it was most numerous in Minsk district, and later in Gomel'sk, Mogilevsk and Vitebsk districts (Table 12).

In the central chernozem districts, not long ago wolves were quite common. Relatively large numbers were noted in 1951–1953 in Voronezh and Belgorodsk districts (Barabash-Nikiforov, 1957).

In southern Bashkiriya at the edge of the upland-forest landscape in the forest-steppe, wolves were few in the 30's. About 1950, they were quite often encountered, but in the upland broad-leaved forests, they became scarce in winter (Kirikov, 1952). Wolf numbers here are sharply reduced. In Volzhsk-Kamsk territory, from 1950 to 1965 wolf numbers sharply decreased. In Tatariya during the five years from 1960–1964 the average annual production of skins was 170 (140–186, V.A. Popov).

In the Ukraine, the wolves multiplied during the war years, 1941–1945. In 1947–1949 their numbers in the entire Ukraine reached about 7000. Population density was low in those places where villages were closely situated (Korneev, 1950). After 1945, wolves were frequent in the southern part of Sumsk district (especially in more wooded regions). In Chernigovsk district, which is very suitable for wolf habitation, their high numbers were retained the entire time and in 1938, 110 animals were caught here. After the war, especially many appeared in Chernigov Poles'e; fewer in the forest-steppe and southern regions. In Kievsk district, the predators became numerous in its northern, forested sections. They were occasionally captured in the regions adjoining the Poltavsk and Chernigovsk districts; in Kievsk district, wolves were noted in a series of southern regions. In

Table 11. Manufacture of wolf skins from eastern Siberia (Khudyakov, 1937)

Regions \ Years	1932	1933	1934	1935	Average, %
Main Western	398	315	309	292	11.0
Eastern	1478	1175	905	1369	42.4
Remote taigas	16	7	20	17	0.6
Northern	38	33	46	89	1.7
Buryat ASSR	1636	1186	1266	1239	44.3

Table 12. Average annual output of wolf skins per 1000 hectares in Belorussia (Serzhanin, 1955, with modifications)

Districts \ Years, data	1932-1939		1948-1952
	Average by district	Fluctuation in various regions	Average
Brestsk	—	—	0.5
Vitebsk	0.1	0.8-0.02	0.3
Grodzensk	—	—	0.5
Gomel'sk	0.2	0.8-0.03	0.3
Minsk	0.3	0.8-0.03	0.4
Mogilevsk	0.1	0.3-0.03	0.4
Molodechnensk	—	—	0.4

Zhitomirsk district, wolves were restricted to the northern regions, along the border with Belorussia (Korneev, 1950).

- 151 In the western districts of the Ukraine, wolf numbers are generally not great. They are higher in western Poles'e, in Rovensk and Volynsk districts. There are many wolves in the montane regions of former Stanislavsk district. In the Trans-Carpathians and in L'vovsk district, the wolf is rare; in Ternopol'sk district, it does not live permanently, appearing periodically from the southern regions of Rovensk and the northern regions of Stanislavsk districts (Tatarinov, 1956). In L'vovsk district, wolf litters were noted only in the Kamensko-Bugsk, Sokal'sk and Peremyshlyansk regions. In the Trans-Carpathian area, they are relatively common in all montane and low-lying regions (except rocky places in the high mountains). Stray wolves were met with in the Vinogradovsk, Uzhgorodsk, Perechinsk and Mukachevsk regions. In Drogobychsk district, wolves are common in montane regions; in 1949 litters were encountered in the Turkovsk and Podbuzsk regions, and strays in the Strelkovsk and Dorogobysk regions.

In Stanislavsk district, wolves occupy permanently the southern and southwestern montane region, and intrude on the plains. In Chernovitsk district, wolves occur permanently in five southwestern regions bordering Romania, and also in Sakyrsk and Kal'menetsk regions, where they often come from Moldavia.

In Kamenets-Podol'sk district, wolves are established in the northern regions, but animals are scarce here. In Vinnitsk district, wolves are regularly noted only in two southern regions; they penetrate hither from Moldavia, where there are many wolves. In Kirovogradsk district wolves are more or less constantly present in the Pri-Dneprovsk regions adjacent to Kiev district. In Poltavsk district, wolves live in the eastern regions (near Sumsk district), and penetrate along the forested massif into Mirgorodsk region; they were also found nearer to Kiev district.

In Khar'kov district after the war, wolves propagated more in the central regions. Very few litters were found in the Volchansk region, and in the Kupyansk region vagrant wolves were recorded. In the Lugansk district, wolves were present in 31 out of 34 regions; they were especially numerous in the northeastern regions. In six of these, in 1949, 150 wolves were captured. In Donetsk district, wolves are rare and noted only in the south. In Dnepropetrovsk district after war, wolves lived permanently only in the extreme eastern regions. In Zaporozhsk district, wolves live mainly in places near the Dnepr floodlands, and appear occasionally in the Berdyansk and Pri-Azovsk regions.

In Khersonsk district until 1948–1949, the Tsyurupinsk and Skadovsk regions were densely inhabited by wolves; on the right bank they were totally absent; after 1948, they appeared in the Khersonsk, Berislavsk and Novovorontsovsk regions. In Nikolaevsk district, wolves live permanently in the Shirokolanovsk region; strays appear in the western regions. In Odessa district, wolves are common in the western regions. In 1949–1950, strays were also observed in the central regions. In the Izmail'sk region, wolves live permanently in the regions adjacent to the Moldavian SSR. In the floodlands of the Dnestr, wolves are few (Korneev, 1950). In the Crimea, wolves were exterminated, but during the years of the Patriotic [2nd World] War, they appeared again on the peninsula; they were soon destroyed.

In the Caucasus, the wolf is distributed everywhere, though not evenly. According to the data on tanned skins, the greatest number of individuals per unit area was captured in the western Cis-Caucasus and eastern Trans-Caucasus. In the 1930's of this century in Azerbaidzhan,

were caught per 1000 km², 11.6 wolves; in Armenia—9.9, in the northern Caucasus, 6.7; in Dagestan, 6.7; and in Georgia, 0.8 wolves. The lower Terek, Sulak, Kuma and the coast of Kyzylagachsk Gulf were the least densely populated by the wolf. In alder bogs of Kokhida, wolf is common in the lower Gagid, Okum and Picher rivers. In montane regions of the Caucasus, wolf numbers are high in the Caucasian, 152 Borzhomsk, Zakatal'sk and Lagodekhs preserves (Vereshchagin, 1959). In the Trans-Caucasus, wolves are everywhere, but along the wooded Black Sea coast they are so rare that they were never seen by the majority of inhabitants (Satunin, 1915).

In Kazakhstan, the wolf is encountered nearly everywhere. Their numbers are highest in the west, in several regions of Aktyubinsk and Kustanaisk districts, in the valleys of the Syr-Dar'ya, Chu, and Ili rivers, and in the mountains and foothills of the Zailiisk and Dzhungarsk Alatau, near Lake Kurgal'dzhin, in the Alakul'sk depression, around Zaisan Lake and in several other places. In the northern forest-steppe regions, wolves are scarcer. However, in the former Kustanaisk district of the former Turgaisk governance, their number in beginning of the twenties was extremely high (see beyond, V.G. Heptner). In clay deserts and semi-deserts, where there is neither water, wild ungulates or livestock, these predators are absent or appear there only from time to time. There are also no wolves in some of the montane taiga regions of the southern Altai, for example, in the Zyryanovsk region, where snow cover is deep and porous (Afanas'ev et al., 1953). The general number of wolves in Kazakhstan is estimated at approximately 25–30 thousands. About 10 thousand wolves are exterminated annually in Kazakhstan; i.e. a little more than one third of the population (Afanas'ev, 1955).

In Kirgiziya, wolves are encountered everywhere. They are most numerous in the regions of large high montane pastures-elevated watersheds, since in these places not only many livestock are found but also great marmot colonies were preserved, and in the neighboring ranges, large numbers of wild ungulates (arkhar sheep and wild goats). Each year in Kirgiziya, prior to the Great Patriotic War, up to 400–600 wolf skins were tanned (Kuznetsov, 1948).

In Uzbekistan, there are few wolves. In Kashkadar'insk district they are rare; they are rarely met with in desert regions, even in winter; in montane regions, they are numerous (Meklenburtsev, 1958).

In the Turkmen SSR, the distribution of wolves is restricted by the presence of water sources and the abundance and also availability of

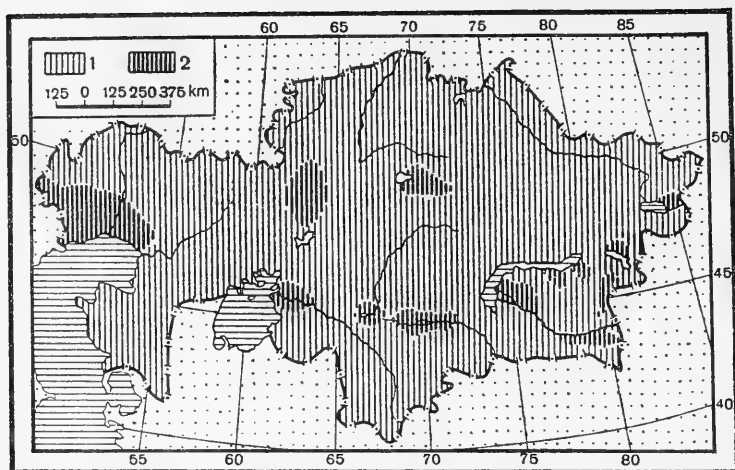


Fig. 54. Relative number of wolves in various parts of Kazakhstan (from Afanas'ev et al., 1953): 1—general distribution, 2—districts where wolves are especially numerous.

food. In Badkhyz (southern Turkmeniya), there are more wolves, apparently, than in other regions of Turkmeniya, which is explained by the abundance of wild and domestic ungulates. The especially large number of wolves between the Tedzhen and Murgab has already been shown by Radde and Walter (1889). Along the Kushka river wolves frequently hunt near the most remote villages. Along the Egrigek river, there are more wolves than along the Kushka; although here there are no human settlements and livestock, dzheiran gazelles [*Gazella subgutterosa*] are numerous, which come to the river for drinking and there are also abundant watering sites and convenient places for dens and diurnal lairs. In Gyaz'-Gyadyk, wolves are common in the whole region. There are many wolves along the Tedzhen river. In the desert part of Badkhyz, the wolf is everywhere, but is unevenly distributed, being concentrated by wells, in grazing sites of sheep flocks and near waterholes, especially those situated not closer than 100–200 m from domiciles (earthen huts). Six to seven wolves on average are associated with one waterhole. In winter, wolves are evenly distributed in Badkhyz, because of the reduced need to drink and the wider pasturing of the sheep flocks (Heptner, 1956). The number of wolves in western Turkmeniya is high, but there distribution is uneven.

It is difficult to estimate, even approximately, the general number of wolves in USSR, not only because of the absence of data, but also

because of uninterrupted changes in their numbers. In the 1930's, their number in our country was estimated by a series of authors to be 60–80 thousands, a figure which was, apparently, an underestimate. At nearly the same time, S.A. Buturlin evaluated the wolf population as being not less than 100,000 individuals, and the yearly production as 47,000. After the Patriotic War of 1941–1945, the number of wolves markedly increased, particularly in the regions which suffered from the German invasion. After restoration of the destruction caused thereby, as a result of augmented wolf control and the application of a series of very effective means for their extermination (shooting from aeroplanes and airosled*, etc.), the number of wolves was reduced in the 1960's by not less than 3–5 times and in places, more. In a series of districts they disappeared entirely.

One may establish several general laws:

1) The highest numbers of wolves are in so-called “open” landscapes—southern tundra, forest-tundra, forest-steppe, steppe and several desert regions.

2) Within these zones, the distribution of the predators and their mode of life, in particular nomadism, depends upon the allocation of the chief foods—wild and domestic ungulates.

3) In the forest zone, especially in the taiga, the most important obstacle for wolves reveals itself to be deep, porous and prolonged snow cover, which sharply limits the possibility of movement and capturing food. The rarity or absence of wolves in the deep taiga regions, which is a consequence of this situation, was already established by A.F. Middendorf (1869)** and later confirmed by all investigators. However, a clear coincidence between the snow cover depth and the abundance of wolves cannot be established, since the relation here is more complicated; in actuality, the influence of snow on the number of wolves acts through a complicated system of biological relationships and essentially changes through the direct and indirect effects of human activities.

The construction of roads and paths increases the possibility of wolf movements, while the added complexity of the landscape and the appearance of farming and animal husbandry in these regions enriches the potential food reserves, especially in winter time. This explains the direct relation that is manifested between the number of wolves and the agricultural development of the territory in little-developed taiga regions.

*Forerunner of snowmobile—Sci. Ed.

**Not in Lit. Cit.—Sci. Ed.

In many poorly inhabited regions of taiga, there are no permanent wolf populations and the animals only rarely intrude into these places by chance. In such unfavorable and almost uninhabitable territories, wolves penetrate mainly along the river valleys with their rich and complex biocenoses and their greater degree of development of places suitable for humans.

- 4) In the desert-steppe regions, the presence of watering places serves as the important factor limiting the number and distribution of wolves, being quite necessary for the predators, especially in the hot time of the year. There, concentration of the animals is noticeable near wells and in river valleys, where they find, not only the necessary water, but also abundant food since in such places both wild and domestic hoofed animals are concentrated.

Habitat. Places of diurnal rest, where dens are also located during the reproductive season, are usually especially well protected and are characteristically near watering places. The hunting territories of wolves are various, and are restricted only to the possibilities of capturing food.

On the tundra, places of diurnal rest of wolves are restricted mainly to river valleys and thickets in dry plateau sections; in the forest-tundra, forest clearings and osier-beds and thickets of dwarf arctic birch serve this purpose. In the Yamal and Bol'shezemel'sk tundras, wolves construct dens, mainly among bushes in valleys and more rarely in the dry meadows of slopes; they use flood terraces and dry osier-bed thickets along drainage divides. Of 11 biotopes in river valleys, wolves use three, and on interflaves of dry plateaus, of 17 biotopes, they are distributed in only one (dry shrubs along the divides; Sdobnikov, 1937). Wolves colonize sea coasts only residually*, where they often feed on marine flotsam (Sokolov, 1951).

In the forest zone, wolves avoid monotonous dense forests. In the taiga of West Siberia, they live chiefly in the river valleys (floodplains) (Laptev, 1958). In the Irkutsk district, they prefer places where small sections of forest alternate with fields, and in winter they use roads and paths laid out by humans widely (Timofeev, 1941). In the Karelian ASSR, wolves live mainly near populated places, in cut-over forests and shrubs adjoining fields. In winter time, they not only approach populated places, but often enter them (Marvin, 1959). In Byelorussia, avoiding the large forest massifs, they prefer small dense plantations with thickets (Serzhanin, 1955).

*The Russian word *gushcha* (sediment, dregs) is used here—Sci. Ed.

In heavily settled regions, wolves, though living in the immediate neighborhood of villages, stay in especially secluded places: forest islands, bogs, remote ravines and gorges, and dense growths of shrubs; at the same time, they often live in vacant weedy field, and sometimes in crop fields (Mertts, 1953).

In the steppes, wolves spend the day, and in the reproduction season construct dens, in growths of shrubs and the remote ravines and gorges overgrown by weeds, among *tugais* [riparian thickets] in the valleys of rivers and streams, in the old weedy fallow fields and in crop fields. In western Kazakhstan, wolves are common in summer in reeds by water bodies, in ravines and sand hills, if there are waterholes there. In winter, they concentrate near livestock pastures, in reeds along the banks and by large lakes, and also near villages, where they feed on carrion and hunt dogs. In northern Kazakhstan, wolves live in narrow gorges, in vacant lands among weeds, and in forest clearings choosing elevated, drier places. In winter they spend the night there and generally remain close to human settlements which they approach by night, while during the day they hide in weeds or reeds by lakes (Afanas'ev et al., 1953). In the Kustanaisk intact steppes, they find shelter in growths of dwarf almond (*Amygdalus nana*) and steppe cherry (V.G. Heptner).

In the deserts and semi-deserts of central Kazakhstan, wolves are restricted in the warm time of year to *melkosopochniki* near springs and streams, in deep *sayakhs** (ravines and valleys) if water sources are found in their bottoms, in weeds by water bodies and in forest islands. In winter, they concentrate in regions of livestock husbandry, near rivers and lakes, or they follow the herds of saigas and dzheiran [*Gazella subgutterosa*] (in Betpak-Dala).

In southern Kazakhstan, especially numerous are wolves living in the river valleys (Aksu, Karatal, Ili, Chu, Talas, Syr-Dar'ya). In summer, they are found in the tugais, reeds and rose willows at the lake channels, and rarely in the stabilized sand hills near water. Here, many wild pigs, roe deer, hares, pheasants and waterfowl are found year-round; here also domestic cattle graze. In winter, the wolves move, by night, from the river valleys to adjacent regions where domestic cattle and dzheiran winter, but at daybreak they again return to the valleys. In the sands, wolves only occur near waterholes, constructing dens in saxaul forests or in dense growths of shrubs (Afanas'ev et al., 1953).

*Foreign (Turkic?) word—Sci. Ed.

The distribution of wolves among the biotopes in other desert regions of Middle Asia is the same. In Turkmeniya, the wolf is widely distributed, but is obviously attracted to human settlements and places where domestic livestock graze. It is encountered high in the mountains (2000 m above sea level and higher), in sandy and clayey deserts and cultivated landscapes. In intense heat, wolves are almost absent deep in the desert, or they are rare and are restricted to only the few wells which are used by people where there are sheep flocks and also water remaining from the drinking places of the herds. The animals occur mainly along the river valleys near the watering places of wild ungulates (mainly dzheiran) and domestic cattle. In winter, when the wild ungulates and herds are distributed throughout the whole desert, wolf distribution changes accordingly (V.G. Heptner).

In the mountains, the wolf ascends to a height of 3 and 4 thousand m above sea level (Pamir). In the mountains, the thick and very snowy cover favors wolves because they, in following ungulates, stick to less snowy slopes and those blown free.

In the northern Caucasus, wolves prefer inhabited places, and in remote places, are met with only where there are many wild ungulates. The life of the wolf here is closely connected to the domestic animal herds, especially sheep flocks, in the following of which the predators ascend the mountains in summer and in winter, descend (Satunin, 1915). In the Caucasian preserve, 30% of the incidence of wolf encounters were in the alpine zone, in dark coniferous forests, 32%, and in the broad-leaved forests, 38% (Teplov, 1938).

In Armenia, the wolf inhabits the dry subtropics, semidesert, montane and meadow steppes, sub-alpine and alpine meadows, and also encountered in barren mountains, cliffs and talus, and do not avoid cultivated lands. Within the boundaries of Armenia, the wolf is met with at heights of 560–3800 m above sea level. In summer, a greater portion of the wolves hold to high mountains, in places where domestic cattle graze, and are in small number in the desert and barren mountain zones. By winter, wolves descend to the valleys and only a few of them remain in the mountains near herds of wild ungulates (Dal', 1954).

In the mountains of Kazakhstan and Kirgiziya, wolves remain in summer in alpine meadows, abounding in marmots and wild ungulates, and where the domestic animals pasture at this time. In the upper reaches of montane rivers (at heights of 3000–3500 m above sea level) wolves also raise their cubs at this time. After the development of snow cover in the mountains, following the wild and domestic ungulates, they

descend to the foothills and valleys; only a small number of them remain near the herds of wild, and sometimes domestic, ungulates, remaining in the mountains in winter in the heat of the sun in sunny and wind-blown areas (Afanas'ev et al., 1953).

In Semirech'e there are, apparently, two populations of wolves; one lives in the mountains and descends in winter together with the ungulates, wintering in the foothills, while the other—the plains population—occupies in summer impassable thickets of sea buckthorn, tamarisk, and other shrubs in the tugais. Both populations are associated with flocks of sheep and wild ungulates (Shnitnikov, 1936).

Food. The wolf is a predator, the main food of which consists of mammals of moderate and large size. Almost everywhere it is associated with the ungulates comprising its main food. The quantity and accessibility of it determines the predators' numbers. Upon the life characteristics of the ungulates depends also the way of life of wolves, differing in different regions because, first of all, the species composition and biology of the wild ungulates or the methods of keeping domestic animals in these regions are not the same. If not fundamental, then of significant importance in the nutrition of wolves are animals of medium and small size—marmots, hares, badgers, foxes, polecats and others. In many places, wolves successfully hunt dogs, and, in the regions where raccoon dogs are acclimatized, they are destroyed in great numbers by them. Among small mammals, wolves catch ground squirrels, mice, hamsters, voles and other rodents, and also insectivores. In the agricultural forest-steppe and steppe regions, wolves eat small rodents in the fields. They successfully hunt waterfowl, especially during the time of their molt. Large birds, mainly egg clutches and young, suffer from wolves. Wolves destroy many domestic and wild geese. Reptiles (lizards and snakes), frogs, rarely toads, and also large insects are eaten by wolves when other foods are insufficient. In times of hunger the predators readily eat carrion, visiting cattle burial grounds, slaughterhouses, tallow-presses or especially situated lures. If such places of carrion deposition are permanent, they can determine the winter route of wolf packs.

In many, if not all, regions, wolves are partial to plant as well as animal food. They willingly eat berries of mountain ash, lily of the valley (*Convallaria majalis*), bilberries, blueberries and cowberry (in the forest zone), nightshade (*Solanum nigrum*), fruits of apple, pear and others (in the south). In summer, they readily visit melon fields, eat watermelon, muskmelons and frequently cause great damage, not only

by eating the fruits, but many others are spoiled. They frequently eat various grain crops, and in the Pri-Ural steppes, the delicate and sweet shoots of reeds.

Cannibalism is not rare among wolves. In times of hunger in winter, the pack often attacks weak or injured animals. They may attack a male, which in its struggle for a female, becomes severely wounded. In captivity, cannibalism is noted during the transition of young wolves from meat to milk or vegetable foods. The stronger cubs attacked and ate the weak (Barabash-Nikiforov, 1957). Hungry wolves fight fiercely for food, and frequently kill the weaker ones, which are afterward almost always consumed. Cases are described when wolves killed and ate the wounded or the dead bodies of their kin (Makridin, 1959). Therefore, these animals are generally not fastidious about food, but when possible, they eat only the best food; this is particularly related to the summer time and concerns plant foods, the need for which is not so large.

The wolf is an animal of great endurance. It is able, without losing strength and running speed, to survive prolonged hunger, for a week or more. But upon succeeding in a hunt, it is very voracious and, according to some authors, can eat immediately a large quantity of food—up to 25 kg, as if laying in a store (Manteifel' and Larin, 1949; Timofeev, 1949; Semenov, 1954). It was noticed that a litter of 7–10 wolves completely consumed an entire horse carcass during one night (Sokolov, 1951). In the lower Ili river (Kazakhstan) a pair of wolves ate a roe deer weighing 25–30 kg or a young wild swine of 30–40 kg at one time (Afanas'ev et al., 1953). In Badkhyz (Turkmeniya) a wolf was observed to devour a young arkhar sheep of about 10 kg in weight (Heptner, 1956). However, these amounts do not characterize the quantity of food actually eaten at one time. A part of this food is usually pulled apart and hidden away, especially when there is plenty of food. At the same time, animals torn apart by wolves are often further eaten by hyaenas, jackals and especially vultures. In Badkhyz, a skeleton of a donkey which was torn apart by a pair of wolves at the start of night, was found in the morning completely cleaned of meat (Heptner, 1956). More than 1.5–2 kg of food can be rarely found at one time in the stomachs of wolves (Novikov, 1956). According to the accurate data of P.A. Martts (1953), a wolf eats no more than 3 kg of food at one sitting and any excess amounts are quickly regurgitated. The relatively small amounts of meat eaten by a wolf at one time is also to be understood by the figures given above on the weight of wolves (p. 174).

The foods of wolves vary substantively in the various seasons, and these changes are associated with changes in the life habits of the predators—their transition from a settled life in the warm time of year to a nomadic way of life in winter. In summer, various foods are available for wolves, and its quantity is maximal in this period. Therefore, summer feeding of wolves is diverse. The principal share in various regions is occupied by different foods, but mainly by animals of medium and small size. The significance of ungulates is reduced in this period, although wolves still hunt them. Thus, in the stomach of a young wolf killed on 3 July 1944, in the Bashkir preserve, remains of a young maral [*Cervus elaphus*], a mole's foot and 2 nestling sparrows were found; and in the stomach of a juvenile wolf caught on 17 August 1941, 16 lizards were found. In the valley of the Ural river, wolves in summer frequently visit melon fields and eat watermelons, and in the Shaitantau [mountains] during a year of steppe-cherry harvest, its stones were found in the majority of the wolves' feces (Kirikov, 1952). At the end of summer and the beginning of autumn wolves hunt pastured livestock and wild ungulates, catch hares, dig up muskrat burrows and houses, catch the small animals and birds, and around water bodies, successfully obtain molting waterfowl.

After snow accumulation, feeding worsens. At this time, the principal attention of wolves is directed to ungulates. In the time of greatest hunger, wolves approach populated areas, hunt dogs, attack livestock in their sheds even by day, and willingly make use of cattle burial grounds and carrion.

In winter, wolves travel along roads and unwillingly turn into the snow upon the appearance of not only a single sledge but even a series. At this time, wolves also attack elk*. However, the attack by an individual wolf of an adult elk, especially in more or less deep snow, often ends in the death of the wolf. For instance, in the winter of 1952/1953 in Verkhne-Toemsk region of Arkhangel'sk district, two wolves were found killed by elks (Semenov, 1954). An attack by a pack usually is successful. In March–April, in the forest zone on crusted snow, wolves rarely appear near the villages and mainly travel through the forests, hunting roe deer, elk and [rein]deer on the snow crust.

Early spring (after the crusted snow) is the time of greatest hunger, when wolves are very harmful to animal husbandry (especially in the steppe), exterminating mainly the young. Chiefly at this time in the

*In North America, called "moose"—Sci. Ed.

steppe and desert, but also in tundra, wolves hunt pregnant ungulates (dzheiran, saiga, roe deer and [other] deer). At the time of birth of the young, wolves gather near the place of calving, where they kill both adults and young.

After melting of the snow and the beginning of spring reproduction of animals (end of April–May) wolves transfer their feeding mainly to vertebrates of moderate and small size. In June, the young begin to feed mainly on animals, and the mother's milk is only a secondary food for them. In June, wolf-cubs already can walk independently to water-holes. From August on, attacks of domestic livestock become common (Khudyakov, 1937).

The food habits of wolves in different regions differ markedly. The food of tundra wolves during the snowy period is without exception wild and domestic [rein]deer (mainly calves and does). They attack hares, arctic foxes and other animals. In the Nenetsk Nat. Okr., in the stomachs of 74 wolves caught in winter and spring were found remains of: reindeer—93.1%, small rodents—5.4%, willow grouse—4.1%, white hare—1.3%, foxes—1.3% and fish—6.8%. Of great importance in the life of wolves living at the expense of ungulates is the group attack and mass “cutting” of the prey into [smaller] flocks and herds. Later, wolves often travel to places of these “foragings” to utilize the preserved remains. Small groups of predators remain near the sea coast or by villages where they feed on marine flotsam along the shore, the wastes of industry, carrion, and rob the traps and snares of hunters (Makridin, 1959).

In the summer food habits of wolves on the tundra, a considerable role is played by birds (in the second half—especially molting geese and ducks) and small rodents (lemmings and voles). [Rein]deer, especially at the beginning of summer (calving time), also play an important
 158 role. In the montane regions in the northeast, snow sheep, hares and marmots occupy a notable place in the food habits of wolves (A. Romanov, 1941).

In the taiga of Karelia, wolves attack elk (young), reindeer and domestic livestock and eat carrion; in summer, they catch rodents, ground nesting birds, and sometimes lizards and frogs. They also eat berries, in autumn especially mountain ash (Marvin, 1951).

In the forest of the Tatar ASSR wolves feed in the snowy period mainly on mammals (98% of occurrences), especially the domestic animals, and carrion (68%), followed by mouse-like rodents (24%) and hares (21%). The proportion of birds constitutes only 10% of the findings (as % of total number of stomachs, feces and food remains

investigated; V. Popov, 1952). In the region of the Rybinsk reservoir, wolves in winter hunt mainly elk (Kaletskaia, 1953). In the Urals, they feed on wild ungulates, hares, ground squirrels, domestic animals and birds. In winter, they eat carrion and frequently pursue foxes (Shvarts, Pavlinin and Danilov, 1951). In Belovezhsk Forest, they hunt chiefly wild ungulates (48%), especially wild boars (21%), roe deer (18%), [red]deer (6%). Remains of domestic animals were encountered in 28% of the stomachs. They frequently catch brown hares (16%). In the warm period of the year, the significance of ungulates decreases to 40% (in spring) and 31% (in autumn). At the same time, the role of domestic animals in their food increases from 32% to 42% (sheep particularly are caught). Wolves here hunt dogs relatively rarely (Gavrin and Donaurov, 1954).

In the forest-steppe of the central chernozem regions, domestic livestock, hares and small rodents comprise the principal food of wolves.

In steppe regions, in 56 cases (stomachs, food remnants) first place was occupied by mouse-like rodents (35%), then carrion (17%—mainly in the winter), dogs, calves, sheep, goats, swines (16%). In the stomachs, remnants of hares (8%) and ground squirrels (5%) were often found; in one case, red fox. Proportion of birds (mainly domestic geese) constituted 4%. Occasionally wolves eat lizards and insects (dung beetles). Plant food are represented by berries, strawberries, pears and apples (windfall). In the Usmansk forest, the usual prey of wolves consists of deer, beavers, hares and raccoon dogs (Table 13). In summer and autumn, remains of dogs (38%), hares (18%) and sheep (13%) are found in their food (Mertts, 1953).

Vertebrates are encountered in 92.2% of the cases in food habits of Ukrainian wolves (Korneev, 1950).

159 Foods consist of mammals—90.7% occurrence, birds—12.9%, reptiles—5.5%, amphibians—29.6%, fish—18.5%, insects—46.2%, plants—48.1%. Among mammals, domestic animals are encountered in 48.9% of occurrences, and game species in 32.6%, including hares—22.4%, roe deer—10.2%, mice—14.2%, voles—42.8%, shrews—6.1%. Among domestic animals dogs occupy 18.2%.

Up to 10 water voles (*Arvicola terrestris*) and 15 common voles (*Microtus arvalis*) were found in the stomach of one wolf. An especially great importance in the food of wolves is assumed by small rodents in the years of their mass reproduction (Migulin, 1938). Among birds, mallard (*Anas platyrhynchos*)*, domestic hens and geese

*Sic: should read *platyrhynchos*—Sci. Ed.

158 Table 13. Food habits of wolves in the Usmansk forest (112 stomachs and 63 feces, Mertts, 1953)

Season, data Food type	Winter		Summer	
	Number of occurrences	%	Number of occurrences	%
Deer	37	21.1	3	5.3
Beavers	27	15.3	3	5.3
Hares	34	19.4	10	17.9
Mouse-like rodents	14	8.0	5	8.9
Raccoon dogs	7	4.0	1	1.8
Domestic dogs	20	11.4	21	37.5
Sheep	7	4.0	7	12.5
Swine	4	2.2	1	1.8
Domestic birds	4	2.2	3	5.4
Carrion, bait	17	9.6	—	—
Plant remains	5	2.8	2	3.6

predominate, among reptiles—lizards and among amphibians—toads. Among fish, the pike (*Esox lucius*) was found, being caught by wolves in water-meadows (in times of flood). Other kinds of fish are caught along the shore. Among insects, beetles (100% of occurrences), Orthoptera (48%) and Hymenoptera (44%) predominated. Among the plant food, berries of buckthorn (*Rhamnus cathartica*; up to 389 in one stomach), black-berried nightshade (*Solanum nigrum*; up to 9082 seeds in one stomach), berries of lily of the valley (*Convallaria majalis*; up to 486 seeds in one stomach) and fruits of pear (*Pirus communis*; 140 seeds in one stomach) were met with (Korneev, 1950). In addition to animal foods, many grains of maize were found in wolves' stomachs in the Caucasus, and in Kiev district, the fruiting bodies of mushrooms of the genus *Tricholoma* (Korneev, 1950).

In the Caucasus preserve the frequency of occurrence of various groups in the food of wolves was as follows (Teplov, 1938): mammals—90%, ungulates—81%, wild boar—38%, deer—16%, tur—12%, chamois—12%, roe deer—7%, rodents (hares and mouse-like)—90%, carnivores (bear, fox, marten)—3%, birds (chiefly Caucasian black-cock)—7%, fruits including berries (pear, apple sweet cherry, viburnum, blackberry, dog rose)—12%.

In the Uralo-Embensk desert, the summer feces and food remnants of wolves (268 examples) consisted of 37% mouse-like rodents, jerboas—9.1%, ground squirrels—13.6%, hares—2.6%, hedgehogs—2.9%, domestic livestock—8.8%, birds—15.8%, reptiles—0.3%, insects—1.1% and plant remains—5% (Kolosov, 1935).

In the northern zone of Kazakhstan the prey of wolves in summer are small rodents (especially water voles), hares, young and molting ducks, young blackcocks and willow grouse, and rarely roe deer and domestic livestock (sheep). During times of drying-out of lakes, water birds and water voles are especially available to wolves and hence become the principal food, on which they also feed their litters of whelps. In Kazakhstan the wolves also readily eat the fallen apples and pears, and visit melon-fields. In winter in northern Kazakhstan, wolves hunt domestic livestock, roe deer and eat carrion (Afanas'ev et al., 1953). Around Lake Kurgaldzhin, wolves live all year round in the reeds. In summer they feed on water voles and waterfowl, especially during the time of molt. In winter, they live at the expense of wild pigs, following them in paths which the swine tread in the snow.

In the Betpak-Dala desert, wolves feed in summer on dzheiran, saigas and hares; they also eat gerbils, jerboas, turtles and insects. In autumn and winter, the saigas and dzheiran which overwinter here, as well as the domestic livestock suffer greatly from wolves. Mammals predominate in wolves' food in southern Pri-Balkhash (92–100% of occurrences), among them ungulates (16–100%) and rodents (10–84%) predominate. Among ungulates, wild swine (10–50%) and roe deer (5–100%) are of greatest importance. The wolves frequently eat tolai hares and muskrats. Around water bodies, they eat fish (mainly carp). Rarely they attack foxes, and among birds, mainly waterfowl and pheasants (Table 14).

160 In the lower Ili river the infrequent remains of domestic animals in wolves' food is explained here by the abundance of wild foods. Feces containing soil indicate the necessity to wolves of *melkozem* [fine earth] especially during the transition from summer foods to winter ones and vice versa (Afanas'ev et al., 1953).

Domestic animals have important significance in the food habits of Turkmenian wolves; as does the wild fauna, especially ungulates which play a great role, particularly for the Badkhyz wolf population (southern Turkmeniya). This is, obviously, connected with the richness of Badkhyz in wild ungulates. The particular attention of wolves here is concentrated on dzheiran as the largest amount of the more available species. Adult dzheiran are caught mainly at waterholes by wolves concealing themselves behind dense thickets. Cases of attacks on kulans by wolves are also known, especially during winter snowfalls and on ice-covered ground. Small animals, especially reptiles, are known to be significant in the food habits of wolves in the Badkhyz (Heptner, 1956).

Wild ungulates (goats, arkhar sheep, roe deer, maral) and domestic livestock serve as the main food of montane wolves in Kirgiziya. Wolves follow them into the high mountains in summer, and in winter, they descend to valleys. In summer, wolves readily and successfully hunt marmots, concealing themselves and waylaying them; they eat also small rodents, birds and carrion (Kuznetsov, 1948). In the Dzhungarsk and Zailiisk Alatau, the marmots frequently serve as the main food of wolves (Afanas'ev et al., 1953).

Change in the quantity of the chief foods or the conditions under which it is obtaining in different years strongly changes the character of wolves' food habits. In winters with much snow and particularly with severe and protracted snowcrust, wolves sometimes almost completely exterminate the wild ungulates (especially roe deer), even over great areas. Thus, during the winter of deep snow in 1940/1941 in northern Kazakhstan, wolves almost exterminated roe deer in Kustanaisk, North-Kazakhstansk, Pavlodarsk, Kokchetavsk, Akmolinsk, and East-Kazakhstansk districts entirely. In the Presnogor'kovsk region of Kustanaisk district alone, remains of more than 300 roe deer killed by wolves were found in this year. In Naurzumsk preserve mass mortality of roe deer was noticed after the occurrence of a strong snow crust (16th March). This recurred in the snowy winter of 1948/1949. In the winter of deep snow in 1947/48 wolves attacked even adult male wild boars which they do not try to touch under ordinary conditions (Afanas'ev et al., 1953). Frozen ground and protracted continuous snow cover* in the steppes and deserts and the crusted snow in the forest zone show similar effects. In all cases, the number of ungulates sharply decreases and in subsequent years its significance in the foods of wolves decreases.

In some conditions, wolves feed on completely unlikely food. Thus, during the mass outbreaks of locusts in the Kizlyarsk steppe in the 1920's, the feces of wolves consisted entirely of the remains of these insects (V.G. Heptner).

Home range. The way of life of wolves and their methods of utilizing territory differ in different seasons and are not the same in populations inhabiting different geographical zones and regions. Everywhere, two main seasons are distinguished, when wolves lead differing mode of life. In the warm period of the year, in the time of parturition and rearing the cubs, adult wolves live in pairs (families), while *pereyarki* (young of the previous year) [yearlings] live singly or in

*In Russian, *dzhut*—Sci. Ed.

small groups, usually not far from the parents. Both groups are fully established or accomplish only short migrations mainly at the end of the season.

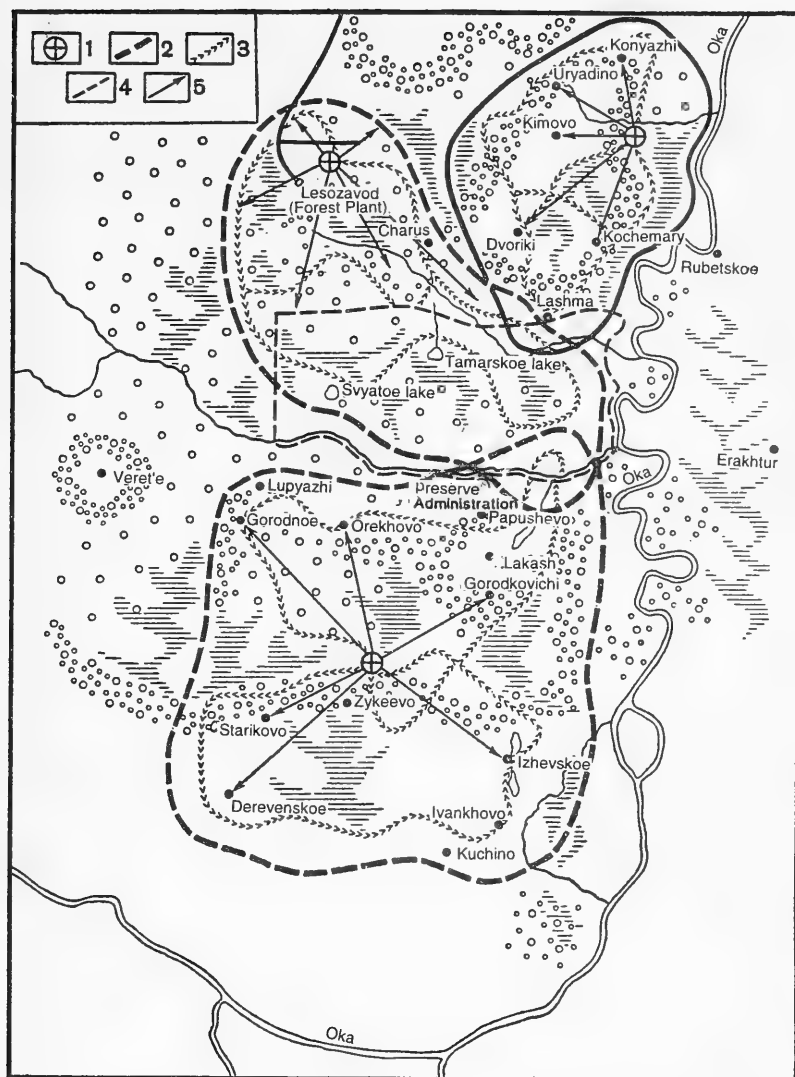
By the cold time of year, the yearlings join the adults with this year's young. Thus a "pack" of wolves is formed, representing, in fact, a family group consisting of the parents, juveniles (this year's litter) and yearlings which have not yet reached sexual maturity. It more rarely happens that older animals, usually males 3–5-year old, which have been left alone for one or other reason, join such a "pack". Strange animals, born to other parents, are not admitted into the pack and are regarded as enemies.

The average size of a pack is 1–2 adults, 3–6 juveniles, and 1–3 yearlings, i.e., 5–11 beasts. The largest pack known was composed of 16 beasts (2 adults, 10 juveniles and 4 yearlings). On the European tundras, packs are usually composed of only the parents and young—mostly 5–7 animals (maximum 10 wolves). Apparently, on the tundra, yearlings do not always join their parents (Makridin, 1959). In Arkhangel'sk district, the pack is usually composed of 7–8 and rarely of 10–12 animals (Semenov, 1959). In wolf packs in eastern Siberia, there are usually 7–10 animals (Khudyakov, 1937; Timofeev, 1949). In Ryazansk district, in a total of 14 years of observations only once was a pack of 11 encountered (1946), and 2 times of 10 wolves (1945 and 1947; Kozlov, 1955). In Tatariya, over several decades of observation, no pack was found consisting of more than 12 wolves (V.A. Popov). In Belovezhsk Forest, where wolves were numerous, a pack of 12 wolves was found in 1946. Apparently, in this region, packs of 15 and 16 wolves may be present, but more often, they consist of 8–10 animals (Serzhanin, 1955). In Kazakhstan, 3–12 wolves occur in the pack, and rarely—15. In the lower Ili river, packs of up to 10 wolves are met with (Afansa'ev et al., 1953) (Table 15).

162 Table 15. Number of wolves in a pack in the lower reaches of Ili river

Time of observation	Number of wolves										Total of packs	Average size of pack
	1	2	3	4	5	6	7	8	9	10*		
October–December	8	4	6	3	3	—	2	1	—	28	28	3.3
January	14	6	1	—	—	—	—	—	—	21	21	1.4
February	2	3	3	—	—	—	—	—	—	8	8	2.1

*Figures in this column are clearly in error; they should be (from top down) 1,—,—.
—Sci. Ed.



162 Fig. 55. Hunting areas of wolf pup litters in winter in Ryazan district in the region of Oka preserve (from Kozlov, 1952).

1—location of litter, 2—hunting area of litters, 3—consistent passage of wolves, 4—preserve boundaries, 5—migrations of wolves for prey in summer.

The average number of cubs in a pack in Aktyubinsk and North-Kazakhstansk districts in December–January was 6.3 animals (of seven packs; Afans'ev et al., 1953).

- 162 The pack is sometimes divided into groups. Thus, in the winter of
 1944/45 a pack of 10 wolves, living in the region of Oka preserve, was
 often divided into two groups, each of 5 wolves, hunting independently
 at a distance of 8–10 km from one another. One group was led by the
 163 mother and the other by the father (Kozlov, 1955). The winter pack
 completely dissolves only with the deaths of both parents.

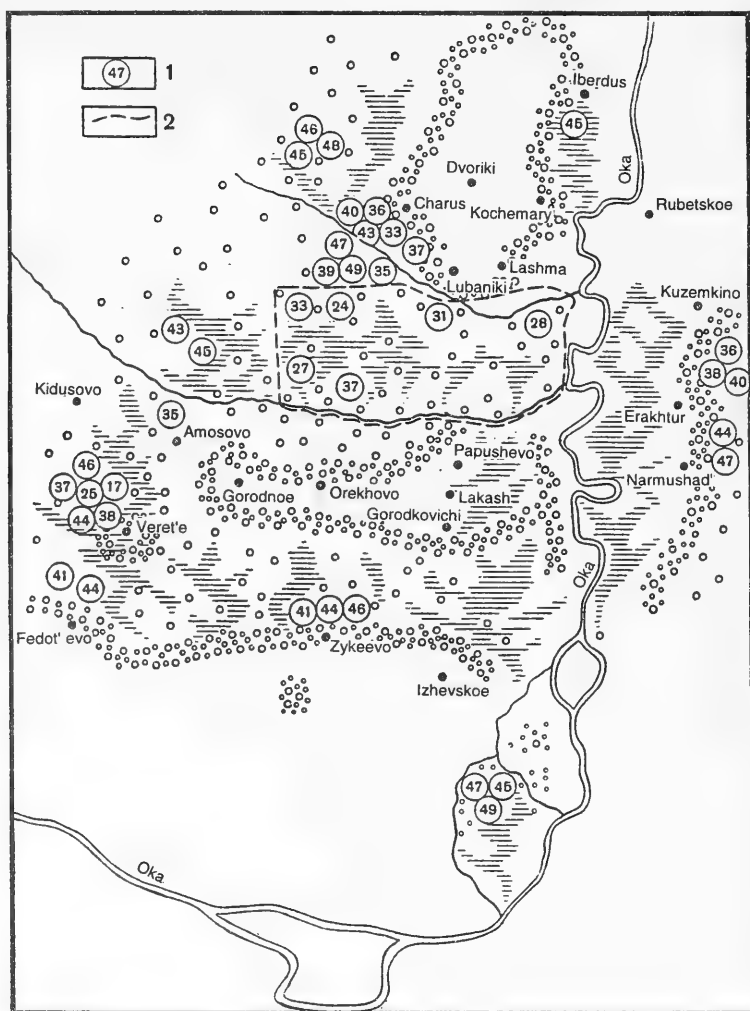


Fig. 56. Distribution of wolf pup litters in the region of Oka preserve (Ryazan district; after Kozlov, 1952).

1—place and year of litter, 2—preserve boundaries.

On the tundra, wolves feeding on prey from the traps of hunters, carrion and bait at villages or edible flotsam by the sea, do not live in packs, but singly or in pairs. Packs apparently cannot be sustained on such food (Makridin, 1959). Old wolves incapable of reproduction live also alone in winter (Kozlov, 1955). Sometimes, killing of weak or diseased animals is observed in the wolf pack. Thus, wolves usually tear apart and eat an animal which eats a strychnine bait and goes into convulsions (Shvarts, Pavlinin and Danilov, 1951).

As a rule, packs live separately and on meeting, they relate to one another with hostility, although cases of serious clashes, fights, or especially "battles" are unknown. Wolves which enter into the hunting territory of a strange pack of wolves leave it at once upon their first meeting with the owners of the territory, or upon discovering their "scent marks" (see below). In rare cases, separate packs temporarily
 164 unite and together attack a herd of wild and domestic ungulates; in this case, the size of the united group may reach 20 and more animals. Such a union is always transitory and of short duration, and usually happens in places of crowding of ungulates—near large migrating herds, in the places of mass calving, and so on. In the Mongolian Republic, such joining of wolf packs was observed around large herds of dzeren



Fig. 57. Birch clear-cut in steppe—denning place of wolves. Krasnoyarsk territory. May 1959. Photograph by V.V. Kozlov.

[Mongolian gazelle, *Procapra gutturosa*] (Bannikov, 1954). During periods of pack life, wolves without growing young are very active and in some places perform extensive wandering, following the migrating wild ungulates or herded domestic livestock.

In the second half of winter and to its end, the mothers with their by this time maturing yearlings separate from the pack and wander in pairs or groups. The young wolves with the still not mature yearlings in the lead, remain together, and in their absence, they disperse into groups of 2–3 animals or wander singly.

The summer sedentary life of wolves begins, in the middle zone, usually in April, with the arrival of pregnant females at den sites. Whelping places (dens) are permanent; they are only changed in case of extreme necessity, particularly alterations in the surrounding landscape unfavorable to wolves. The den is situated either at the center or in one of the parts of the hunting territory of the family (see below). Pregnant female wolves usually return to their old dens, while the young that are pregnant for the first time, search for new lairs which are, as a rule, not far from the place of their birth. At that particular time the winter packs of wolves finally break up and the juveniles, having now become yearlings, separate from the parents and live independently, usually not far from the mother's den.

Different wolf families have mutually exclusive hunting territories, and the simultaneous living of two families in one territory is, as a rule, impossible. Under certain conditions, at least in winter, this rule is, however, not followed. Thus, in winter of 1920/1921, at the time of great food scarcity (*dzhut*), a great number of horses wintered on pasturage in glades in steppe areas and large meadows among the clear-cuts of the Ara-Karagai forest (b. [former] Kustanaisk, Turgaisk governance). The wolves, numbers of which were especially high in that year, gathered thither from a large region and killed the horses. The number and density of wolves in Ara-Karagai was so great that there was no separation of hunting territories of the packs and permanent packs were not really present (V.G. Heptner).

The territory of the pack and its boundaries are distinguished by special characters—scent marks—places where wolves urinate. They are usually situated near things—rocks, boulders, a single tree, the skull or skeleton of a large animal—that are easily distinguishable from afar. On passing by such a place, wolves must visit them and leave their own marks, indicating that the spot is occupied. These “urine points” are the best places for setting traps.



Fig. 58. Small cliff in the forest-steppe under which was a den with 6 wolf pups. May 1958, town of Khakassiya, Krasnoyarsk territory. Photograph by V.V. Kozlov.

The size of the hunting territory of the wolf family, and consequently the distances between summer dens, depends on the availability of food in the territory (stocks of summer food of wolves), cover, and many other conditions. In the middle zone, dens are located usually no closer than 6–12 km from each other (radius of the hunting territory is 3–6 km; Kozlov, 1955). In the Ukraine, summer hunting territories of wolves are smaller. Dens here are situated near one another, sometimes in neighboring ravines or in one woodlot (Korneev, 1950). Exceptionally, two female wolves sometimes give birth to their young in a single den. Thus, in the Sinyavsk region of Sumsk district in 1948, 8 wolf pups and 2 old female wolves were found in one den. Among the cubs, four were noticeably larger and obviously belonged to another litter than the other four (Korneev, 1950).

In the taiga of eastern Siberia, the average radius of the hunting territory is approximately equal to 10 km in summer (Khudyakov, 1937), while in steppe and especially in desert zones it is larger and the wolves' dens are located no closer than 15–20 km from one another. Only a few exceptions are known. Thus, in the Vishnevsk region of Karagandinsk district, three burrows of wolves were found at a distance of only 500 m from each other. Two pups were found in one

burrow, 5 in another and in the third, 6 pups with eyes open were found (Afanas'ev and others, 1953). In the middle zone, cases are known (very rare) when two litters lived at a distance of only 2 km from each other. These were 2 female wolves with their young, the males of which
 166 (both) died in the spring (Sokolov, 1951). At the same time, there is some indication that when neighboring dens are close, the female wolves ate each other's young (Danilov, 1945). In the mountains, dens are, as a rule, located nearer to each other than in forest steppe and desert zones.

At the time when the juvenile wolves are present in the den, the parents usually do not hunt in the immediate neighborhood, but go out to the farthest parts of their hunting region. Thus, in 1942 in the Altai, in snow which had fallen on May 20th it could be traced that parents went a distance of 12–25 km from the den for their prey, at a time when wild ungulates and grazing livestock were living in their neighborhood



Fig. 59. Tracks of two wolves, passing a day lair, the place of their daily rest. Khakassiya, Krasnoyarsk territory. 12 December 1956. Photograph by V.V. Kozlov.

(Nasimovich, 1949; Afanas'ev et al., 1953). In the middle zone, the radius of summer hunting chases does not exceed 5–10 km (usually 5–6) (Sokolov, 1951). Thus, in Ryazansk district, in the period when the young are being fed, the adult wolves hunt usually no closer than 5–7 km from the den and do not touch livestock grazing within the limits of this zone. In the summer of 1939 in the Charussk forestry [area], a den of wolves with a litter was found 1.5 km from Chernaya Rechka village; livestock from this settlement were pastured in the immediate proximity of the place of the litter, but no losses caused by wolves were noticed. At the same time, complaints about wolves were constantly being lodged from those who were raising livestock at a distance of 7 km from the litter's location. After destruction of the litter, there was not even one case of attacks by wolves on livestock. Only yearlings sometimes break the "rule" of not touching livestock near the den of the wolf family (Kozlov, 1955).

In a convenient den, located in a favorable place, the litter lives the whole time until autumn and the beginning of the nomadic period. However, if the den is established by the adult wolves far from a water source (2–5 km away), it is used only until the young are weaned from the mother's milk. Later, the litter resettles nearer water. The particularly great need for water is manifested in the young at their transition to a meat diet. Upon the drying up of a water source, wolves also lead or transfer the young to a new den. During a period of drought in Kazakhstan, wolf pup litters are concentrated near the few intact water sources, devastating their neighborhood, while some litters perish due to starvation and especially the deficiency or absence of water (Afanas'ev et al., 1953).

A den-burrow built in open, non-overgrown ravines is also changed. It is only used so long as the wolf pups do not come out of the burrow. Later, the parents lead the litter to more hidden places (thickets of shrubs and weeds, forest islands and sometimes to winter crop fields where bread grain is grown)*. In the Oka floodplain, the adult wolves frequently led the growing litters to places with an abundance of small fruits—raspberries, strawberries, red billberry [*Vaccinium vitis-ideae*] and others (Kozlov, 1955).

- 167 The she-wolf sometimes builds a temporary nest for whelping, particularly when the places of the main nests are flooded by melt-water, or when the she-wolf is frightened in some way before parturition

*Probably refers to winter wheat—Sci. Ed.

from the main nest. The duration of their stay in the temporary shelters is determined by the local conditions, but before the young of the current year become independent of their mothers, the litter usually changes several temporary dens. In these cases, the she-wolf accompanies the young to the main lair when they are already quite independent (Sokolov, 1951).

If wolves in a den were disturbed, particularly if their litter was touched, they usually abandon the den, carrying the surviving young to a new place. With closing of the entrance to the den (burrow), the parents usually dig it out at night and carry off the pups. At such times, neither the female or male wolf defend the nest and do not attack its invader, even if the nest is destroyed and the pups taken (Kozlov, 1955). While the adults are busy raising the litter, the yearlings remain in the region of the litter, but they do not approach the den closely. They live alone, or in groups of 2–3 animals and hunt independently.



Fig. 60. Resting place of wolf in forest-tundra. Photograph by V.P. Makridin.

At the start of raising the litter, the old wolves remain extremely secretive; they usually do not howl in the region of the den until July. In June in the south, and in July in the north, the demands of the young for food noticeably increase, and the parents significantly expand their hunting territory. Precisely at this time, the young begin to give voice, apparently because above all they often feel hungry. After the young develop, their elders begin to howl upon their return from the hunt, and the juveniles answer the old ones. At the same time, cases of attacks by wolves on livestock become more frequent in the vicinity of the den. Thus, in 1938 in Kalininsk district, a horse was killed only 500 m from a den, and the she-wolf for several days led the litter to the carcass to feed. Near Bologi, a maturing litter of wolves assiduously tore up sheep and calves, not farther than 2 km from their den (Sokolov, 1951). Beginning with this period, together with the young (juveniles) may be found the yearlings which join the family till the time of the next rut. In July (in the south) and August–September (in the north) the maturing young wolves attain half the size of the adults and begin to participate in the hunt with their parents.

The size of the hunting territory continues to increase in autumn, and the wolves gradually convert to a wandering life. Henceforth, the old wolves stop bringing food to the den; on killing a large prey, the parents lead the young to it, and after satiation, the family returns to shelter by the morning (Khudyakov, 1937).

When the milk teeth of the young are replaced by permanent ones, the wolf family begins to hunt together. At first, however, wandering is restricted to the hunting territory. Roaming increases with the fall of snow and the termination of livestock pasturing. In the middle zone, the family rarely returns to the den site in the winter, establishing instead diurnal lairs (Kozlov, 1955).

In forest regions of Arkhangel'sk district, from September wolves already lead a nomadic way of life, making long movements and spend the day where they are met by the dawn. At this time, each wolf family occupies a definite hunting region, leaving it only in case of prolonged and sharp hunger or continuous pursuit by humans. Tundra wolves are, at this time, still more active. In eastern Siberia in winter, wolves wander widely, following wild ungulates, mainly roe deer. Beginning in November, they hunt ungulates almost exclusively; making chases or driving the roe deer onto the ice, capturing them in their beds; and frequently bringing *izyubr* [Manchurian wapiti] to "bay". These predators do not remain for long in one place; the hunting territory of the pack sometimes reaches a diameter of 70 km (Khudyakov, 1937; Timofeev, 1949).



Fig. 61. Tracks of a pair of desert wolves, hunting a saiga. Central Betpak-Dala, Kazakhstan. 7 January 1957. Photograph by A.A. Sludskii.

169 In the central districts, during snowy periods of the year, the hunting region of a wolf family is also expanded. In Ryazansk district, the family hunting range of wolves had a diameter of 25 to 40 km. In forest and forest-steppe districts of the European part of the USSR, wolves in winter perform movements of about 15–30 km during the night and when hungry, up to 50–60 km (Kozlov, 1955). In Voronezh and contiguous districts, wolves leave the permanent summer habitats in November, when the radius of their hunting activity does not exceed 5 km and begin to wander widely, dividing up into small groups, carrying out invasions of livestock yards. At this time the radius of their hunting range increases to 15 km and more (Mertts, 1953). In forest-steppe regions, the greater part of the animals concentrate in forests, where in winter the food is more abundant, and they usually occupy permanent hunting ranges. With the coming of spring, they again wander back to the fields (Mertts, 1953; Barabash-Nikiforov, 1957).

Pack formation in the snowy time of year makes it easier for wolves to obtain food, especially the young (see below). In places with deep porous snow cover, the pack moves in a line, always with an adult wolf in front. In places with little or no snow, for example in the lower



Fig. 62. Tracks of a desert wolf following a saiga. Betpak-Dala desert, Kazakhstan. 19 December 1956. Photograph by A.A. Sludskii.

Ili river, the pack frequently moves in a helter-skelter fashion (Afanas'ev et al., 1953).

In searching for prey, wolves move around their hunting range along a definite route (Fig. 55), using one and the same trails for extended periods, restoring them after snowfalls; during this, the wolves without fail find their old tracks, and follow them exactly, track by track. Trails are laid out along the banks of rivers and shores of lakes, in places of passage between plantations, ravines overgrown with shrubs, etc. Widely used are roads and paths made by humans (Semenov, 1954).

Wolves on the tundra lead a pack way of life for the greater part of the year, because attacks on [rein]deer herds and the pursuit of stragglers from the herds are more successful when hunting in a group.

In the taiga zone also, particularly in the second half of winter, wolves do not often find prey sufficient for feeding the whole pack, and thus, cooperative hunting becomes temporarily unfavorable, and the wolves hunt in pairs or singly, gathering in the pack only for diurnal rest. Sometimes the pack is broken up and for a week or two the wolves live in collections of not more than 2–3 animals (Semenov, 1954).

With the beginning of the rut, the mature wolves drive away from themselves the young and yearlings that up till now have lived with them. After heat which continues for 5–10 days, and the end of rut, the wolf family gathers together again for a short time for cooperative hunting of large prey. In the north, approximately in April, such packs
 170 gather on the main trails along which the [rein]deer herds move to their summer pastures, and in following these herds, they move to the tundra and to places of littering of the young.

Burrows and shelters. Different protected places serve as diurnal lairs (resting places) for wolves. In cold, windy and damp weather, the wolves prefer the more protected places, while in dry, calm and warm weather, they willingly lie down in the open. In autumn–winter–spring period, when the wolves lead a nomadic, or in general a more active mode of life, they lie down wherever they are at daybreak. In summer time, they are associated with dens which they must build for the young (see above).

In constructing the den, the she-wolf usually makes use of natural shelters—fissures in rocks, cliffs with overhangs by the banks of rivers and slopes of ravines, holes thickly covered with plants, thickets of saplings or bushes, “brushwood”, or fallen branches, weeds, etc. In many cases the nest is constructed in the burrows of various animals—foxes, badgers (in the forest zone), marmots (in steppes, montane meadows), arctic foxes (in tundra), etc. Wolves usually widen the adopted burrow and partly remake them. In rare cases, the she-wolf digs a burrow, which is usually shallow and short, with 1–3 openings. The burrows are built on hillsides with soft, mainly sandy and sandy loam soil. In the majority of cases, the carnivore’s nests are situated in dry sections.

The den, as a rule, is constructed not more than 500 m from a water source (lake, river, creek, spring, deep hole with water, pond, etc.); to it one–two trails lead, becoming especially noticeable when the young begin to leave the burrow. The approach to the water source is often concealed. Near the trails around the den, a large number of resting places of wolves, places of play for the cubs, and food remains

are encountered. From the den there usually emanates a sharp odor of urine and of rotting food remains. The food remains attract such birds as magpies, ravens and others to the nest. By their cries, it is possible to locate with precision the nests of wolves with litters.

Convenient places for dens are few, and from year to year they are occupied usually by one and the same pairs of wolves. If the male dies, he is replaced by a yearling in the pair, and if it is female—by a young she-wolf. Empty dens are therefore rare, and they are only left due to the fundamental changes in the conditions of the surroundings (felling of the forest, fire, marsh drainage, etc.). Thus, in the Charussk forestry [area] of Ryazansk district, wolves established a den for four successive years (1936–1939) in one and the same woodlot, although every autumn a drive was mounted against the litters appearing there, when a portion of the young were killed, and in 1937 the mature male was also killed (Kozlov, 1955).

The wolves more frequently select for dens, places rarely glanced at by humans, but they construct them near domiciles, paved roads, railways. In 1941 a wolf's nest with young was found within 200 m of the Moscow-Leningrad highway (Sokolov, 1951). In Zheltukhinsk region of Ryazansk district, a she-wolf built a den in part of a field overgrown with weed only 1.5 km from the village. Another wolf den was discovered 10 m from the road-bed on the Moscow-Ryazan railway, under a pile of snow-screens (Kozlov, 1955). A she-wolf with a litter lived in the middle of a peat-bog not far from a corduroy road along which carts frequently passed (Manteifel', 1949). In Ryazansk district a den was found in a small but dense birch clear-cut not far from a large village (regional center of Erakhtur) and in immediate proximity to a large road with much automobile traffic (V.G. Heptner). In the depth of large forest massifs, wolves do not usually make dens. In Tatariya, all lairs were situated not further than 500 m from the forest edge, usually along ravines where there is water (V.A. Popov).

171 In different landscapes, the situations and construction of dens are somewhat different. Tundra wolves use shelters of three types: a) land burrows, which they build themselves or adapted from ones of foxes, and rarely, arctic foxes. The burrow consists of an entrance trench 1.5 m in length, an underground corridor 50–60 cm wide, and length 2 to 10 m, and a nest chamber $150 \times 100 \times 70$ cm; the chamber is situated at a depth of 1.5 to 3.5 m, and usually contains no nest bedding; b) burrows under rocks of nearly the same construction, but usually shorter; c) different natural shelters (caves, fissures in rocks, etc.). The wolf



Fig. 63. Tracks of a wolf and a she-wolf. Uzhursk region, Krasnoyarsk territory.
December 1957. Photograph by V.V. Kozlov.

den is usually situated on the southern and south-eastern slopes of river banks or hills; they are better warmed by sun, and the snow thaws more quickly there (Semenov, 1954).

On the Kaninsk tundra, wolves are mainly confined to hills in summer. In Lena-Khatanga territory, burrows are usually no longer than 1.5 m and not deeper than 1 m (A. Romanov, 1941). In Anadyrsk territory, wolves give birth to pups mainly in land burrows (Sokol'nikov, 1927).

In the northern forest districts, wolves settle on dry ridges in the middle of marshes, on islands of coniferous forest with abundant fallen branches in coniferous saplings. They prefer burned-over mossy bogs, especially in the difficult-to-penetrate margins overgrown with impass-

able small trees. Wolves settle in wet areas covered with alder woods and on islands of dry, but dense, forests with spruce understory, which are rarely visited by humans (Semenov, 1954).

Wolves living in the forests of Ural and Siberia, usually have dens for their litters situated directly on the surface of the earth, under bushes, overthrown trees, etc. With wolves of the open steppes and forest-steppes, the denning place is more often built in a burrow, as a rule in a foreign one—usually of fox, badger, or marmot (Khudyakov, 1937; Shvarts, Pavlinin and Danilov, 1951; Laptev, 1952). In the steppes, burrows were also found distant from water sources—up to 12 km (Borzinsk steppe). They were constructed in open, usually elevated, places. In southeastern Siberia, a wolf den was found on a promontory by some falls where only a few birches grew, but, it was dry there and the she-wolf had a good field of vision, which protected it from surprise attacks (Khudyakov, 1937).

In Belorussia, a litter of 6 pups was found in a fallen hollow alder tree on a small hillock in a thicket of small alder trees (Serzhanin, 1955).

172 In the central chernozem regions, dens of wolves are situated in young and old broad-leafed and mixed forest islands, in steppe ravines and gorges overgrown with shrubs, and in reeds and willow thickets in marshes, along the margins of bogs, and sometimes even in old straw stacks and in the remains of corn-shocks. In the steppe section of Voronezh district, the wolves raise their young mainly in “yarugas”—ravines densely overgrown with small oaks. In forests, dens are constructed under uprooted wind-fallen trees, sometimes in burrows of foxes and badgers. In fields, the predators use old military trenches, and in ravines—in holes and cavities.

In time past, there were repeated cases of pups being transferred by she-wolves to tall cereal grains and construction here of dens in the immediate proximity of villages (Mertts, 1953). In the Kantemirovsk region of Kamensk district, in the autumn of 1953, was found a burrow with two exits situated in a rye field where the wolves successfully brought the young. Here such dens are not rare (Barabash-Nikiforov, 1957). In Chernigovsk district, a she-wolf built a den and brought the pups to the hemp plot of a personal holding of a collective farmer 10 m from his house. In the Kovertsovsk region of Volynsk district, a litter of wolves lived in a rye field, 300 m from the cottage. The den was constructed in a hole by the side of an uprooted stump. Such cases are known in Sumsk, Zhitomirsk and other districts. In Donetsk district, a

wolf den was found 150–200 m from a very busy paved road (Korneev, 1950).

In the forest regions of the Ukraine, dens are frequently built on islands among sphagnum and other bogs, in dense undergrowth of saplings and in forest islands with dense shrubbery among fields (Korneev, 1950). In forest-steppe regions, dens are situated in deep forest ravines, in sparse forests along river valleys and in impassable alder wood along tussock bogs (these places are called “volchatniks” [belonging to wolves]).

In forest-steppe zone of Omsk district, the wolf selects for dens ridges among marshes, ravines overgrown with bushes, thickets of sagebrush in virgin land, and forest islands (Laptev, 1958). In the steppe zone of the Ukraine, dens are more frequently present in deserted gorges with thickets of spiny bushes and tall weeds in depressions between sandy hillocks, overgrown by willow and other bushes, while on the floodplain of the Dnepr and Dnestr—along thick stands of reeds and other dense places (Korneev, 1950). In the forest-steppe and steppes of Kazakhstan, den burrows are found in the forest, at the edge, and in open places, usually among tall weeds or bushes at a distance less than 1 km from a water source. In the forest preserve “Borovoe”, a wolf den was situated in a cave on a hill covered by a pine forest; this den was thrice destroyed and near it, she-wolves were twice killed.

Dens dug by wolves in the steppe are usually 2–5 m long, rarely more, with one or two exits, and the nest lies at a depth of 1–1.5 m from the surface. Old, repeatedly used dens have very wide passages through which humans can easily crawl, and several nest chambers; entrances to the old chambers are frequently filled in when wolves prepare a new one. Lairs in the open are established under cover of bushes or tall weeds. In North Kazakhstan district an open lair was found in the reeds of an almost dry lake; the nest was situated in a large opening among meadowsweet [*Filipendula*], around which shallow water was present. Within such a lake, a she-wolf brought a large heap of cattail and reed and gave birth to 7 cubs on it.

In the desert zone of Kazakhstan, wolves give birth to cubs both in burrows and in open-air dens. Burrows in the southern Pri-Balkhash' were found in *solonchaks* [salt flats]. They were 7 and 8 m long and 1–1.5 m deep. In sandy mounds covered with saxauls, a den was excavated at the top of a mound under the roots of saxaul and consisted of a simple niche, in which 6 cubs were lying. One burrow was situated in a dense growth of saxauls in the Ili river valley. Here open-air lairs

were also found in reed growths and under willow bushes (Afanas'ev et al., 1953). In Kazakhstan, of 24 wolf dens, 14 were situated in burrows dug by she-wolves, one was in a badger burrow, another one in a cave, another in a niche and 7 were in the open (in tall weeds, rose willows or reeds).

- 173 In Turkmeniya, wolves inhabit the plains, old stream channels in cliffs of the *chink* along the Uzboi, in ravines of the Kopet-Dag [mountains], near creeks and springs, chiefly in the shady places, under the overhanging rocks, etc. Sometimes, dens are situated in dense growths of tamarisks (*Tamarix*) or other bushes, and often in tugai (riparian vegetation) (V.G. Heptner). In Armenia, these predators usually use narrow caves, fissures and ravines for dens (Dal', 1959).

In the montane steppes of Kirgiziya, on high-alpine watersheds and in the foothills, wolves usually construct the den in a burrow dug in a ravine, under a bush, or in another such protected place. On the slopes of mountains, they use fissures in the rocks, overhanging shelves of stone, marmot burrows, etc. (Kuznetsov, 1948).



Fig. 64. Tracks of a desert wolf in mud near a waterhole in the Gyaz'-Gyadyk mountains. Badkhyz preserve, southern Turkmeniya. February 1965. Photograph by V.G. Heptner.

Daily activity and behavior. Wolves are nocturnal predators. In the majority of places they lead a nocturnal mode of life in summer as well as in winter.

In winter, wolf litters begin hunting in the early evening twilight; they hunt the entire night, sometimes traveling tens of kilometers, but nevertheless often they lie down to their diurnal rest hungry. In sparsely settled regions, hunting during the day is also observed, usually for wild ungulates (Korneev, 1950). In those places where wolves are active only at night, individual wanderers also hunt during the day. Thus, in January 1951, in the region of the Oka preserve, one yearling she-wolf picked out among all prey particularly those that were active by day (V.G. Heptner). Attacks of wolves on livestock were common, and especially on single horses during the daytime, often at the village itself, in the period of their very high numbers at the beginning of the 1920's in former Kustanaisk district of Turgaisk governance (V.G. Heptner). With the arrival of winter, when lying down rather than a bed the wolf turns around until there is no longer any packing of the snow, in order to form a good pit-lair. While sleeping, wolves space themselves in a semicircle, covering their "scenter" (end of



174 Fig. 65. A wolf calmly walking in deep snow. Krasnoyarsk territory. January 1958. Photograph by V.V. Kozlov.

the nose) with their tail. Sleep is very light, the ears are constantly either pricked up or drooping. Wolves sleep especially lightly in times of frost.

In eastern Siberia, in summer, the wolves mainly stick to a nocturnal mode of life, although whelps are frequently active by day also. In autumn, after the transition of the whole litter to a nomadic life, they hunt mainly at night.

- 174 In southern Turkmeniya (Badkhyz), wolves lie by day in tamarisk-like or other shrubby thickets, and sometimes almost at the outskirts of settled places, always relatively close to water sources, but in sandy areas, at a distance of 15 km from wells (Heptner, 1956). In settled regions of Kirgiziya where wolves are frequently disturbed, they mainly lead a nocturnal mode of life; but in remote places, one may see them hunting during the day (Kuznetsov, 1948). Mongolian wolves hunt at any time of the day or night (Bannikov, 1954).

Hungry wolves become aggressive. A huge number of cases are known of severe attacks of wolves on livestock. Thus, on 1 February 1953, two wolves attacked the calf-pen of a collective farm in the Dryazginsk region of Lipetsk district. On hearing the noise, the people came running; however, their appearance did not cause the wolves to run away. A struggle began which ended only after one wolf was struck with pitchforks. In autumn, wolf litters commit audacious onslaughts on herds of sheep and flocks of geese, sometimes seizing their prey almost from the hands of the shepherds. Under ordinary conditions, wolves fear humans and are very cautious. They can well differentiate between dangerous hunter and unarmed herdsmen, in front of the eyes of which they frequently attack the sheep.

Pursued wolves sometimes seek shelter in villages. In 1950, a wolf, having been shot from an airplane near the village of Vyselka Rozhdestvensko—the Khavsk region of Voronezh district, fled to a village and took shelter in the hayloft of a house near which a calf was lying. The wolf was discovered only after some time (Barabash-Nikiforov, 1957). In Kirgiziya, the wolves in winter approach villages and frontier posts even during the day (Kuznetsov, 1948).

Wolves hunt in various ways: from concealment, pursuit of prey, and organized as a drive in groups. In summer they hunt mainly singly, the wolves frequently ambushing their prey, rarely spotting and pursuing prey. When attacking a herd, even individually, wolves try to frighten the animals, creating panic and dispersing the herd or separating one or several animals from it.

175 Upon attacking a herd, wolves are able to distract the attention of the shepherd and often conduct a very well-organized combined hunt of ungulates and hares, in which the functions of each member of the pack are not only different, but also coordinated. Breaking off from one another, they envelop the pursued animal from different sides and at last surround it. Frequently, some of the wolves pursue an animal and another group tries to intercept or set up an ambush in its path (Timofeev, 1949). Once on the Malyi Cheremchan river in Tatariya, there was observed about 9 in the morning a unique hunt by wolves for geese: a wolf drove the swimming geese to a bridge, at which a hidden she-wolf intercepted them (V.A. Popov).

Along black [snowless] paths or in light snow, wolves can pursue prey at a speed of 55–60 km per hour; with this they quickly catch even the brown hare [*Lepus europaeus*] which runs at a speed of 40–45 km per hour. Wolves obtain roe deer by driving them in persistent pursuit. They destroy many marals by chasing them in winter into [soft] sediment surrounding a rock, the predators patiently wait until the legs of the maral stiffen and it becomes unable to remain by the stones. Four–five wolves do not fear to attack an elk on frozen snow-crust, but with little snow, the adult elk is for them a dangerous enemy (see above). The pack can easily cope with young pigs and sows, but they usually fear to attack boar (Timofeev, 1949). Wolves pursue and frequently kill foxes but they rarely eat them. Hence, where there are many wolves, foxes usually become few. In the European part of the [Soviet] Union wolves in winter very successfully lure dogs from villages and catch them by feigning a cowardly flight (Korneev, 1950). Wolves at night, and sometimes during the day, enter villages and settlements. Thus, in August 1954, wolves carried away a sheep which spent the night in the street from the outskirts of the village of Kopanovo (Ryazansk district), and injured another (V.G. Heptner). Wolves follow the barking of the hound dogs for many kilometers and often catch them during the hunting season. In the agricultural central-chernozem [black earth] regions, wolves have adapted to “mousing” behind the tractor ploughs, remaining some distance from it and catching the voles flushed out by the plough (Mertts, 1953).

In searching for prey, the wolves depend mainly on their sight and hearing; scent is relatively weakly developed in wolves, and therefore, they rarely discover hidden hares or birds. But, when they come across a fresh track, they can easily follow it without becoming confused (Timofeev, 1949). Hearing of wolves is very sharp; the organ of hear-

ing is constantly exerted, the wolf hears and constantly registers the fall
 176 of autumn leaves from the trees. It nearly never happens that a sleeping
 wolf can be approached, while it is not very difficult to approach a
 sleeping fox. Only a replete sleeping wolf can sometimes be approached
 to within 10–30 steps.

The sense of smell of the wolf is weaker than that of many hunting
 dogs. The wolf can scent carrion on the wind for not farther than 2–
 3 km. Because of the comparative weakness of their sense of smell,
 wolves can be taken in traps relatively easily. The sight of the wolf is
 not so complete as that of dogs. In darkness, the wolf sees better than
 the other species of the dog family because, through their way of life,
 they are by preference nocturnal animals (Korneev, 1950). Even at



175 Fig. 66. Diagram of the tracks of a wolf
 pack walking, as usual, one behind the other;
 when turning they separated but again went
 one behind the other. The tracks during the
 turn represent the only reliable possibility to
 establish the number of wolves in the pack—
 4 in the present case (from Kozlov, 1955).



Fig. 67. A wolf on guard. Khakassiya, Krasnoyarsk territory. Winter, 1957.
 Photograph by V.V. Kozlov.

night the wolf can easily detect the flaws in disguised traps. At the same time, wolves are far-sighted and they can distinguish between the armed hunter and the simple passerby at great distances. Upon concentrating their attention on any item or occurrence, the wolf considerably blunts its perception of others. Numerous occasions are known when, fleeing from beaters, wolves came very near to shooters, even those not hidden. A wolf may approach with the wind, a person standing motionless especially when dressed in camouflaged clothing up to 5–10 m, not smelling an odor or noticing a motion (Kozlov, 1955).

On the whole, the level of nervous activity of wolves, and their ability to consider situations is quite sufficiently high. The behavior of wolves is more complex and “wiser” than is assumed by the majority of zoologists and hunters. When going to their dens, adult wolves skillfully select hidden approaches. At that time, they make numerous “dodges” and “double-backs” using bushes, wind-fallen trees, stumps and many others. Their ways of hunting, as shown above, are highly variable and they are usually governed by the complex and highly coordinated behavior of the members of the litter (pack). The complex nervous activity of wolves with the highly developed and multiple conditional reflexes (temporal connections) allows them to adapt them-

selves quickly to new situations. This "flexibility" in the behavior of wolves, for example, their ability rapidly to distinguish poisoned baits and avoid them, makes their control difficult.

177 *Seasonal migration and transgressions.* Wolves in the majority of regions are settled. They abandon their accustomed places quite unwillingly, usually only in cases of severe shortage of food in their hunting territory. The migration of wolves is, in the majority of cases, connected with nutrition and represents nomadic movements for food.

Significant seasonal movements of wolves have a place only in tundra, steppes, deserts and montane regions with nomadic (shifting) livestock breeding, where the herds of reindeer, horses and cattle are regularly driven from the summer pastures to winter and vice versa. Examples of such nomadism are performed by herds of reindeer in tundra, saigas, dzerens and goitered gazelles in steppes and deserts, roe deer in the Urals and in Siberia, and by deer in the mountains. The times and paths of migration of the ungulates and the wolves coincide. In mountains, during the fall of deep snow, wolves, following the ungulates, move to less snowy places, usually descending to the foothills.

In the tundra wolves lead a nomadic way of life for three-fourth of the year, not adhering to stable hunting regions. Twice yearly they accomplish large meridional migrations connected with the driving of the [domestic] deer herds. When the deer herders shift southward, the wolves go together with the deer herds to the forest border. They do not, as a rule, penetrate deeply into the taiga, although in the European north in particular, the main mass of the deer herds of the state farms and collective farms winter there. Wolves prefer to remain in the forest-tundra and mossy bogs with less deep and more firm snow cover. Here in the forest-tundra, there is much natural food, since willow ptarmigan migrate thither, white hares are very frequent, and until recently, elk were encountered along the river valleys where trees are located (Semenov, 1954). In the Nenetsk Nats. Region, besides seasonal migrations, the movements of wolf packs from the Bol'shezemel'sk to Malozemel'sk tundra in connection with herd migrations were noted, but return movements were not (Makridin, 1959). Seasonal migrations of tundra wolves in the European north reach 200–300 km (Semenov, 1954).

A small portion of the wolves remains on the tundra in winter. They move out to the sea coast, where remain only small reindeer herds of hunters engaged in the arctic fox harvest and near fishery stations,

feeding on fish and other animal wastes. On the seashore wolves find the bodies of stranded marine animals. Tundra wolves are very mobile and move for great distances. A trailed pair of wolves went 70 km in one night (Semenov, 1954); from an airplane it was possible to follow the path of a pack of wolves that went more than 150 km in 20 hours (Semenov, 1954). Regular migrations to the Novosibirsk islands, following reindeer across the sea ice are accomplished by wolves in northern Yakutiya. In the forest zone, wolves are less mobile. They follow roe deer during their migration in the taiga of eastern Siberia (Khudyakov, 1937). During food abundance, the predators remain for 5–8 days in comparatively small territories; if they do not obtain food, the wolves go “on foot”, moving 25–50 km in a 24-hr period.

In the montane forest landscapes of the southern Urals, wolves migrate with the ungulates in winter from places of deep snow. In Bashkir preserve wolves, together with roe deer and marals, remain in the winter in the montane massif of South Krak and stay in small numbers in the Uraltau (Kirikov, 1952). In the Altai, they leave the mountains following the roe deer into the lower valleys. In the Tien Shan, the predators ascend in summer into the mountains (to high watersheds) following the herds of wild ungulates and domestic animals and they again descend lower when deep snow falls in the mountains.

Generally, settled populations of wolves live in Caucasian, Borzhomsk and Zakatalsk preserves, as well as in the reed beds of the Caspian coast; however, they also perform vertical and horizontal migrations following the wild ungulates. In the remaining territory of the Caucasus, especially in its eastern part, wolves wander after the herds of domestic livestock, ascending the mountains in summer and in winter—to the lowlands (Vereshchagin, 1959).

Wolves accomplish regular migrations in the steppe regions, where transhumant animal breeding exists or where large herds of wild ungulates survive. Following herds of dzeren [Mongolian gazelle] on the [USSR] boundary in the Trans-Baikal steppe, wolves frequently penetrate from the Mongolian Republic. In the deserts of central Kazakhstan, these predators accompany the herds of saigas and goitered gazelles going, in September–October, to wintering grounds in the southern part of Betpak-Dala. From the Severo-Kazakhstansk district, the majority of wolves, in December–April, leave for more southerly regions (Afanas'ev et al., 1953). In the Kustanaisk steppes, in the periods when wolves were abundant in 1920–1921, in autumn they moved about, following

the herds of horses and going by day behind the horse drovers at a distance of only few hundreds of meters or even nearer (V.G. Heptner).

In deserts and in part in the steppes, the cause of wolf migrations may be steppe fires, drought and lack of water or other reasons leading to massive translocation of livestock and the migration of wild ungulates. In connection with fires in the Badkhyz desert and consequent lack of water, goitered gazelles appeared en masse along the Kushka river in June 1942. Following them thither, the wolves appeared. This massive appearance of gazelles, and of the wolves following them was noted in 1927 along the Murgab river. In other desert-steppe regions of such a sort, migration of desert and steppe ungulates to waterholes, in the middle of summer chiefly in the river valleys, are always accompanied by corresponding migrations of wolves (Heptner, 1956).

Besides migrations for food, usually taking the character of seasonal migrations, wolves sometimes perform long, time-consuming massive migrations not having a regular character. They are either connected with unfavorable changes in their principal habitats, or represent the growing cubs establishing themselves.

In some years, it was noticed that tundra wolves migrate in a horizontal direction. Migration of wolves was observed from the Urals, to the Yamal, into the Bol'shezemel'sk tundra; the wolf packs crossed the Malozemel'sk and Timansk tundras and reached the Kanin isthmus. Such migrations of wolves usually coincide with massive migrations of arctic foxes in that direction. A return movement of wolves (from west to east) was not observed (Semenov, 1954).

In Kazakhstan in individual years wolves also perform long and irregular movements. Thus, in January 1941 in Dzhabul'sk district many "Siberian" wolves appeared, which were well distinguished from local ones by their large size and gray color. In autumn 1942, wolves moved en masse from the northern Caucasus, from Rostovsk and Volgogradsk districts into Zapadno-Kazakhstansk, Gur'evsk and even Aktyubinsk districts of Kazakhstan. The large European wolves well differentiated from the small, reddish local ones (Afanas'ev et al., 1953).

Settlement of wolves is easily registered when they enter into places which are unsatisfactory as habitat. Thus, during the summer, wolves penetrate into the taiga of western Siberia from districts comparatively far to the north and south, that are continuously inhabited, for tens or even hundreds of kilometers (Aleksandrovsk region of Tomsk district, upper reaches of the Taz river, to Surgutsk region; Leptev, 1958).

However, when the deep snow falls, they abandon these places or die there. Wolves which in winter inhabit the Berezovskii region of Tyumensk district along the Syn' and Lyapin rivers, migrate in summer to the Urals (Flerov, 1933).

Under difficult conditions lengthy migrations are known. Thus, from 1933 to 1945, wolves four times penetrated over ice to Barsa-Kel'mes Island in the Aral Sea which lies 80 km from the shore (Afanas'ev et al., 1953). In 1938, three wolves walked on ice about 200 km and reached Wrangel Island.

Reproduction. Wolves are monogamous; the united couple usually stays together for life, if one of the wolves does not die. Upon the death of the male or female, as shown above, pairs are quite quickly re-established. Since in wolf populations, males often predominate (Teplov, 1948), unpaired females are a rare occurrence, while unpaired males are quite common; this is related to the later maturity of males. Among 179 wolves caught in traps and from airplanes in the European tundras, 71% were males in 1951–1953 (31 wolves studied); in 1954, 67% males (30 wolves) and in 1955, 50% (72 wolves); the average of all years (133 wolves) was 59% (Makridin, 1959).

Wolves mature at about 2 years; practically all she-wolves become sexually mature at the end of the second to beginning of the third year of life; males in part begin to participate in reproduction in the third, and in part the fourth year of life. Estrus in she-wolves and rut begin usually at the beginning to middle of the second half of the winter. Old, multiparous she-wolves enter estrus first, approximately 2–3 weeks earlier than heat in young, just maturing she-wolves. Before the beginning of rut, as was shown, the wolf pack dissolves. Adults disperse first, then yearlings, and finally juvenile wolves. Later on, they re-unite, but they do not approach the adults and lie separately. Driving away the young, the adult male becomes unusually attentive to the she-wolf, does not leave her for a minute and opens up a path for her in the snow.

Heat in older animals usually proceeds calmly, but in certain (rare) cases it becomes complicated due to the presence of 1–2 unpaired males. Heat lasts approximately 2 weeks. At the beginning of heat and rut in the young wolves, they drive away the juveniles still living with them at that time. Particularly at this time, during the formation of new pairs, the so-called "wolf wedding" is manifested, when a group of males gathers around one female. These "weddings" are accompanied by violent struggles and hard fights by young males for the female. The fight sometimes ends with death and the dead wolf may even be

devoured. Such a group does not remain in one place for long, but wanders widely spending the day in remote places—wilderness, bogs, fir-groves, often wandering the byways, usually at night but sometimes also by day time. The she-wolf bonds with the strongest wolf of this pack and thus a new pair is formed, lasting until the death of one or both “spouses.”

The periods of estrus and rut vary in different regions. In the south, copulation takes place 1–1.5 months earlier than in the north; therefore, the period extends from December to March. In the Karelian ASSR, estrus is initiated at the end of February and in March (Marvin, 1959). In Arkhangel'sk dist[rict], rut begins at the beginning of March in the northern regions, and at the end of February in the southern, while in regions adjacent to Vologodsk district, it begins approximately one week earlier (Semenov, 1954). In the forest-tundra and tundra of Nenetsk Nats. Region, the first female in which ovulation had taken place was caught on the 9th of March. In the period 9 March–14 April, only yearling females were still not ready for the rut (Makridin, 1959). In Tatariya, rut usually occurs in the middle of February. In the middle Urals, wolves copulate in February (Pavlinin, Shvarts, Danilov, 1951). In forested montane landscapes of the southern Urals, estrus in wolves proceeds from the end of February–beginning of March (Kirikov, 1952). In the former Tarsk region, estrus in wolves proceeds from the second half of January–first half of February, and whelping in April (Shukhov, 1928; Kuklin, 1938). In Irkutsk district, estrus begins in wolves at the end of January (Timefeev, 1949).

In Belorussia, rut is initiated at the end of January; it ends approximately at the middle of March (Serzhanin, 1955). In Voronezh district, rut in adults begins at the first, or more often the second third of January. At this time, the characteristic howl of wolves can be heard around dawn, but two weeks later, the breeding pack of one female and 2–3 (here rarely more) male wolves can be found during day. Rut ends at the beginning of February, but sometimes extends to the first half of March. After that, the formed pairs occupy territories, and, in April, the she-wolves give birth (Mertts, 1953; Barabash-Nikiforov, 1957). In Alma-Atinsk district estrus in she-wolves proceeds from December–January. In the lower Ili river, a she-wolf in a state of estrus was caught on 27 January 1949. In northern Kazakhstan, estrus occurs in February–first half of March.

180 The duration of pregnancy in the she-wolf is 62–75 days.

In Nenetsk Nats. Region, the largest number of embryos occurring

in pregnant she-wolves was 9; the average number of embryos was 6.5 per female. From one to nine pups have been found (6.7 per female on the average) (Makridin, 1959). The number of whelps in a wolf litter in Yamalo-Nenetsk Nats. Region is more often 3–4, rarely 5. The usual number of a pack (litter) is 7–9 wolves, including 2–3 yearlings

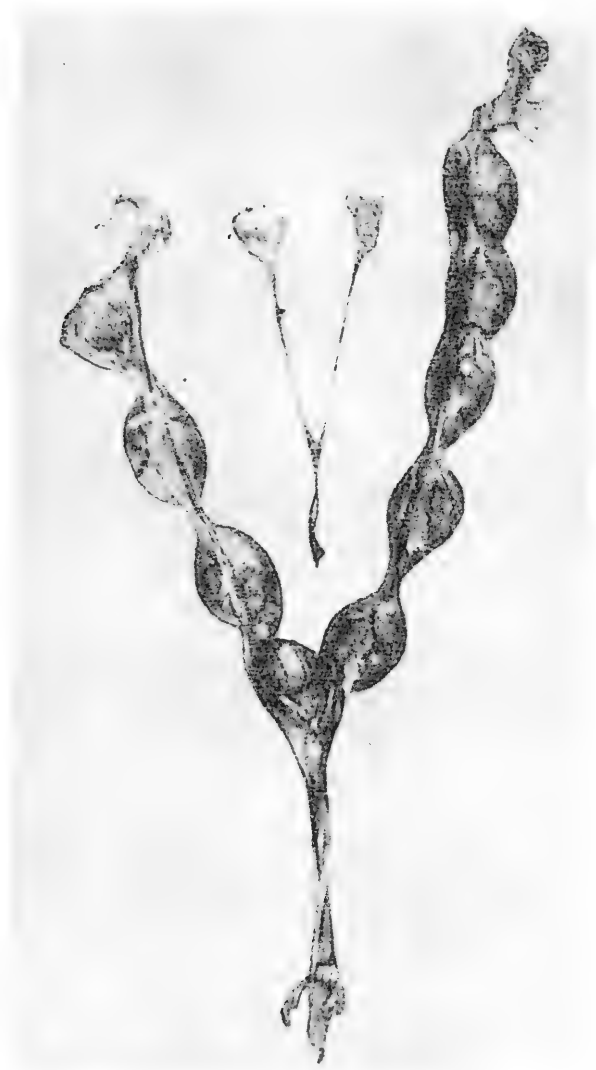


Fig. 68. Uterus of she-wolf with 9 embryos and uterus of a young nulliparous she-wolf, [both] caught in March. Photograph by V.P. Makridin.

(Rakhmanin, 1959). In the middle Urals, there are up to 12 young (up to 14 fetuses were found), more frequently 5–8 (Pavlinin, Shvarts, Danilov, 1951). Young she-wolves produce smaller litters, usually 3–5 young; adults are more fecund (6–8 and up to 14 young). Old females in Belorussia produce 8 young, rarely more, and young—3–5, giving an average litter size of 4–6 pups (see Tables 16 and 17).

The average size of litters varies in different years.

Before whelping, the she-wolf usually returns to the old den in which it has raised the past litter. A young one, whelping for the first time, searches for a new den, usually not far from its birth place.

Parturition of pups takes place in the warm months, when the stocks increase and food becomes varied. In Karelia, 3–7 (rarely more) blind pups are born in April–May or the beginning of June (Marvin, 1959). In Arkhangel'sk district, forest wolves whelp at the end of April and the first third of May. They give birth to 3–12 pups (more often 5–8). In the tundra, pups are born around the second half of May—beginning of June; the young are from 3 to 8, 6 on the average (Semenov, 1954). In the southern Urals, pups appear at the beginning of May. On 21 April 1946 a killed she-wolf had embryos of about 310 gm each (Kirikov, 1952). The earliest litters are found in Belorussia in the second half of March, more often in April and May. In Brestsk district in 1948, pups still blind were found on the 10th, 22nd and 27th of May.

In the central chernozem districts, there are usually 3–4 pups in the litter. In 1950 litters of 6 and 8 pups were captured, and in 1956 a litter of 10 pups. The low average [3–4] litter size in these districts can be explained by the fact that the majority of females die when they are still young, far from reaching the age for which a high litter size is characteristic (Mertts, 1953).

In the Ukraine the pups are born at the middle of March—beginning of April. The earliest litter was found on 3 January 1949, of 5 one-week-old pups (Kiev district). In Sumsk district, two pups approximately 3 weeks old were found on 2 June 1947. In the first third of June, a

180 **Table 16. Frequency of occurrence of wolf litters of various sizes in Belorussia (Serzhanin, 1955)**

Number of pups in litter	1	2	3	4	5	6	7	8	9	10	11	12	Total
Number of litters	5	3	4	10	14	13	6	7	—	1	—	1	65*

*Should total 64—Sci. Ed.

Table 17. Average number of pups in a den (Serzhanin, 1955)

Years	1947	1948	1949	1950*	1951	1952
Number of dens	81	186	150	168	180	173
Average number of wolf cubs in den	4.5	4	4.5	5.2	4.9	4.2

*In Russian original, 1959—Sci. Ed.

Table 18. Frequency of occurrence of wolf litters with different numbers of young in Kazakhstan (Afnas'ev et al., 1953)

Number of pups in the litter	2	3	4	5	6	7	8	9	10	11	12	13	Total
Total number of cases	2	3	7	10	9	12	5	8	2	5	2	1	66
Including:													
In southern districts	—	—	2	2	3	3	—	2	—	—	—	—	12
In northern and central districts	2	3	5	8	6	9	5	6	2	5	2	1	54

litter was found in Chernigov district, and the latest litter was found in Volynsk district in July 1949 (Korneev, 1950). In Zakarpatsk district with its mountainous climate, in the majority of cases birth of the young usually takes place at the end of May. In individual cases, in the Ukraine, litters attain 10–11 young.

In the north and the central districts of Kazakhstan, small pups were found on 16 April (2 litters), from 2 to 30 May (17 litters) and in June (1 litter). From 2 to 13 pups occur in litters, the average litter size in the southern districts of Kazakhstan being 6.3 pups and in northern and central districts, 7.0 cubs (Table 18). A litter of 13 pups was found once, the mother and pups being in extreme emaciation (Afnas'ev et al., 1953).

In southwestern Turkmeniya, the she-wolf produces young at the end of March—beginning of April; on 12 April 1942, blind pups 5–7 days old were caught. In the litter 3–4 pups usually occur (Dement'ev, 1959). In the Caucasus, the she-wolf gives birth to 5–6 pups on the average. Time of birth of pups extends from March to May (Satunin, 1945). In Azerbaidzhan, litters appear in April–May (from 2 to 8 young) in secluded places—remote ravines and in dry islets in marshes (Vereshchagin, 1951). In Armenia, wolves copulate in January, giving birth to cubs in March; the litter is 3–8 young (Dal', 1954).

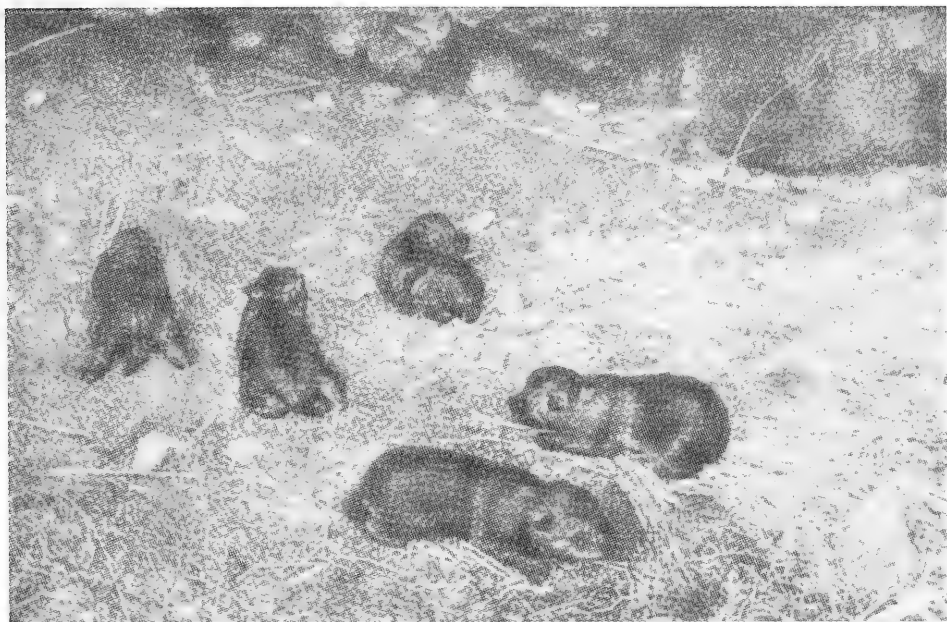


Fig. 69. Wolf pups 10–11 days old, taken away from the den. Khakassiya, Krasnoyarsk territory. 18 May 1956. Photograph by V.V. Kozlov.

Maternal sense of wolves is very strongly expressed. A case is known when a she-wolf followed a hunter who had captured its cubs into a village and at night walked near his house for a long time.

Out of 5–7 pups (average litter size) born, only 1–3 animals reach sexual maturity (juvenile mortality is 60–80%). Wolves usually live not more than 15 years. A wolf which lived for 16 years in captivity was quite decrepit (Afanas'ev et al., 1953).

Growth, development, and molt. Wolf pups are born blind, with closed ear openings, and covered with short soft grayish-brown fur. The weight of new-borns is 300–500 gm. They begin to see on the 9th–12th day; at the end of the second—beginning of the 4th week, milk canines erupt. In captivity, pups which begin to see on the 9th–14th day grow strong and healthy, while those in which vision develops later remain usually sickly and ricketic. 3-week-old pups crawl out of the den, and at 1.5 months old, they quickly flee from danger and take cover. Adult wolves leave their 3-week-old cubs alone when setting out on a hunt.

In the first weeks, the mother does not leave the litter and during this time the father-wolf feeds her, bringing prey to the den, or regurgitating

the semi-digested meat. The she-wolf nourishes the young with milk until they are 1.5 months old. When the pups are 3–4 weeks old, they begin to eat the regurgitate offered by the father, and the mother only eats the remains. The necessity of regurgitative feeding (semi-digested meat) is, apparently, related to deficiencies in digestive juices (peptidases) in the young whelps. Artificially fed pups without such regurgitate are accompanied by poor growth, delayed development and rickets. Pups 3–4 months of age already find such regurgitate unnecessary. In summer, nursing she-wolves become very thin. Milk gradually becomes, for the young, only a supplementary food, and they feed mainly on small animals which the father and mother bring them.

In the first four months, the tempo of growth of the pups is high. During this time, their weight increases nearly 30 times (from 350–450 gm to 14–15 kg; Novikov, 1956). In the southern Urals, the weight of a juvenile male in August 1941 was 11 kg, of a juvenile female—8 kg, in September—13 kg. In the next 3–4 months, the weight of wolves doubles and in December, they reach 28–30 kg (Kirikov, 1952; Gavrin and Donaurov, 1954). In Ryazansk district, young at 6 months attain a weight of 16–17 kg.

Later, when the pups become strong, the mother and father bring living, but injured, prey to them in the den, teaching the whelps how to catch and kill it. At the middle of summer, the adults begin to lead the pups to killed prey. The actual training of the young begins at the second half of the summer. From August, they attempt to catch rodents and other small animals by themselves, and starting from September they share with the adults in hunting ungulates.

The molt of wolves takes place twice per year; in spring from the end of March or middle of April to July. In autumn there is no full replacement of the pelage, only the underfur growing and developing (from the beginning of September to the end of October, and sometimes to the end of November).

Enemies, diseases, parasites, mortality, competitors. This is little studied. The ticks *Ixodes ricinus*, *Dermacentor pictus*, *Sarcoptes scabiei* [the mange mite] and others parasitize wolves in great numbers. In distinction from foxes, only a little full-blown mange is ever observed on wolves; it more often strikes young wolves. Among other ectoparasites may be noted: the biting louses *Trichodectes canis*, the sucking louse *Linognathus* (sp.), and the fleas *Pulex irritans* and *Ctenocephalides canis* (Korneev, 1950). It is completely obvious that this list is very incomplete.

Among endoparasites are established the nematodes *Toxocara leonina*, *T. canis*, the cestodes *Taenia pisiformis*, *T. hydatigena*, *Echinococcus granulosus*, *Mesocetoidea lineatus*, *Diocotophyme renale* (through fish) and the adult phase of the causative agent of sheep gid[diness]—*Multiceps multiceps*. Infections with helminths are not great. In the central chernozem districts, of 20 wolves examined, nematodes were found in the stomachs of seven (4–11 specimens) in the small intestine of one—many fine cestodes, and in the trachea—5 nematodes (Barabash-Nikiforov and Pavlovskii, 1947).

Wolves frequently suffer from rabies and they act as a source of this infection for people. The overwhelming majority of “attacks” of wolves on humans stem from rabid wolves which, because of the disease, lose the caution and fear of man of normal wolves. Although 70–88% of the total cases of rabies among humans is due to bites by dogs, cats—6–8%, and wolves—less than 2–3% (Rudnev, 1950), wolves play the role of principal host (reservoir) of the rabies virus in nature (Zhdanov et al., 1955).

The only serious enemy and competitor of wolf is, apparently, the tiger. In the Ussuri territory, wolves were absent in some places from time immemorial and they appeared only after tigers were exterminated. It was also noticed that wolves disappear from those places in which tigers appear.

The mortality of wolves is great. In the course of the first year of life, as shown, it reaches 60–80%, and subsequently decreases to approximately 40–50% per year. Because of this, young of the current year usually compose about one third of the population (Makridin, 1959).

184 *Population dynamics.* The number of wolves, though relatively stable, changes under the influence of different conditions of existence. It is necessary to accord the first place for significance their pursuit by humans, which increases with increase in density of settlement and the development of agriculture; it becomes weakened when agricultural activity is disturbed for one reason or another. Therefore, a rise in the number of wolves was observed after each war, famine or economic dislocation.

At the beginning of the nineteenth century, wolves were numerous in the majority of the developed regions of the country, including the entire Ukraine both in Poles'e, and in the steppes of the Black and Azov seas. The abundance of predators in the forested parts of the Ukraine was related to the abundance of wild mammals (deer, roe deer,

wild boar, beaver, hares) and birds. The number of wolves particularly increased after the French invasion in 1812 when the numerous bodies along the route of the French retreat served as food for wolves. At that time, there was even noted a migration of predators to Ukrainian Poles'e from neighboring districts of Belorussia (Korneev, 1950). At the middle of the nineteenth century, although the populated areas in the Ukraine increased significantly, wolves remained numerous even in the vicinity of such large cities as Odessa. In only 4 days in the autumn of 1844 during a mass drive in [the former] Khersonsk, Ekaterinoslavsk, Tavrichesk and Bessarabsk governances, 1404 wolves were caught (Brauner, 1923). In the eighties of the past century, there were many wolves in Chernigov governance (Dubyanskii, 1885).

At the end of the nineteenth century, the number of wolves in the entire middle zone and in the Ukraine noticeably decreased. At the beginning of the twentieth century the wolves remained in significant numbers only in districts with large tracts of forests and sparse populations. In [the former] Khersonsk, Nikolaevsk and Odessa provinces, they were completely destroyed, and in the other southern districts wolves remained only in the floodplain of the Danube (Izmail'sk district). At the time of the First World War, the number of wolves grew sharply; this was enhanced by the Civil War and the devastation accompanying it. By 1920, the wolves occupied nearly all of the Ukraine, central chernozem district, the middle non-chernozem zone and the Povolzh'e. In Chernigov district in 1923 alone, wolves destroyed 5.2% of the domestic livestock count. As was noted, wolves were, at that time, very numerous in the north of Kustanaisk district (V.G. Heptner).

In subsequent times, the number of wolves began to decrease and at the beginning of the Great Patriotic War [W.W. II] wolves decreased overall by approximately 100 times as compared to 1920. At this time in the Ukraine, wolves remained only in Zhitomirsk, the southern regions of Kievsk and Chernigovsk, and southwestern regions of Khar'kovsk districts, in the Starobel'sk steppe and in Lugansk district (Migulin, 1938; Korneev, 1950).

New proliferation and recolonization of wolves took place in the years of the Patriotic War, 1941–1945. The number of wolves grew intensively in places where in addition to food abundance, wolves had well protected places for constructing dens. After the Great Patriotic War, the number of wolves increased in all districts without exception, and they appeared in the places where they had been previously exterminated. In the Caucasus, where the number of wolves had increased somewhat

after 1927–1930 and remained at quite a high level until the Second World War, it sharply increased in the period 1941–1945. Only after 1950, as a result of the strengthening of wolf control did their numbers in the Caucasus noticeably decrease (Vereshchagin, 1959).

Thus also proceeded [events] in the European north and in western and eastern Siberia. The distribution of wolves in Siberia was favored by winters with little snow at the end of the 1940's. Wolves became the scourge of [rein]deer breeding in the Katangsk region of eastern Siberia and appeared in the Shitkinsk and Bodaibinsk regions (Timofeev, 1949).

185 After the war, wolf control was sharply intensified, and their number quickly began to decrease everywhere. This was favored by the application of new, totally destructive methods of hunting (see below). In Arkhangel'sk district, intensive destruction of wolves stopped their growth in numbers, and then sharply reduced them. The number of captures per year in Arkhangel'sk district increased from 129 in 1948 to 360 in 1953 (in all 1374 wolves were destroyed in 1948–1953; Semenov, 1954).

In addition to this basic factor in the population dynamics of wolves, great significance must be placed on nutritional conditions in winter and the supply of water in summer. The first is of basic importance in the forest zone and the second, in the steppe and desert zones. However, in the steppe regions of Kazakhstan, the number of wolves also sharply decreases in winters with much snow, mainly as a result of death from starvation. In the winter of 1948/49, which was characterized by strong and prolonged blizzards, wolves were not able to capture food. They gathered near the settled points and somehow fed on dogs, but they quickly began to die (Afnas'ev et al., 1953). At the same time, the widespread opinion that all wolves are obliged to fast in winter is not true. In a pack (family) of two grown-up wolves and four juveniles caught in December 1940 in Moscovsk district (near Maloyaroslavts), the adults were well nourished, but not fat, while the young had good deposits of internal fat which nearly covered the kidneys and a little fat on the thighs. It is evident that the old wolves, even in winter, were solicitous about the better nutrition of the young. Accessible livestock are not here in winter, and only carrion was at the disposal of the pack, apparently, elk, hares and dogs being scarce in the district (in the stomach of one wolf, a piece of leather collar was found; Heptner and Morozova-Turova, 1951). Communications about the capture, in winter, of fat and "very fat" wolves are not very rare, particularly from the tundra (Makridin, 1959).



Fig. 70. Tracks of a pacing yearling female. Oka preserve, Ryazansk district.
15 January 1949. Photograph by V.G. Heptner.

After a series of drought years in semi-desert and desert regions, the number of wolves sharply decreases. Thus, in 1939 in the Ustyurt and Mangyshlak, wolves almost totally disappeared, and in the Turgaisk region of Kustaniask district in 1938, the number of predators sharply
186 decreased. The drying-out there of steppe springs and lakes deprived the wolves of waterholes and the surviving animals concentrated in abundance in ravines at the village of Borgot. In the bottom of ravines, the wolves dug holes, in which ground water gathered, and the animals came regularly to water at these "excavations" (Afanas'ev et al., 1953).

In the drought of 1936, all wolf litters living in the lower Sarysu river and adjacent regions, gathered in small reeds surrounding the two remaining Telekul' lakes. They attacked everything available for them to pursue, but they apparently were starving and the young grew poorly (Sludski, 1937).

Among wolves epizootics sometimes develop, but their causes, course and after-effects are practically unstudied.



Fig. 71. Tracks of pacing wolf. Krasnoyarsk territory. December 1959
Photograph by V.V. Kozlov.

The reproduction of wolves in different years is not the same. In the central chernozem districts, intensive reproduction was observed in 1925, 1934 and 1935, in 1943, 1944 and 1947 (Barabash-Nikiforov, 1947).

Field characteristics. The wolf is a strong, enduring animal; without special effort it can pull or carry on its back a ram. It can move quickly, achieving a speed on bare ground* of 50–60 km per hour (Semenov, 1954). Information about speeds up to 80 km per hour (Nanteifel', 1948) is completely unverified. Usually wolves run at a trot. This trot nonetheless allows them to cover great distances. In this gait, the track of the hind foot falls exactly on the track of the fore, and the tracks are situated, as along a string in one line. During walking, this exactness in the position of the feet is not observed. Wolves of a well-fed pack go in single file, and a tired lead animal is replaced periodically. This allows the pack to move for long distances even in deep snow. Hungry wolves sometimes separate from each other.

When running, the wolf holds its head somewhat low and a little to the side, directing one ear forward and the other backward. This pose gives them the possibility of using their exceptionally sharp hearing. Changing the gait when necessary, the animals switch to a gallop and then a walk; they often stop and stamp in place. In deep snow, they
187 prefer to use roads. By day they go at a walk, avoiding populated places; sometimes dodging and doubling back, like a hare, usually shortly before lying down. Alarmed, wolves may go for 70 km in one night at a trot or jog (Korneev, 1950). Wolves can swim well. In autumn 1948, a litter of wolves regularly swam across the Desna river, on setting out to hunt and on returning from it to the den until a strong cold snap [occurred] (Korneev, 1950). In Ryazansk district in the 1950's, in periods of night hunting, they swam across the swift, wide Oka river to attack the livestock on an island (V.G. Heptner). It is very difficult to catch up with untired animals by rowboat.

The tracks of wolves resemble those of dogs, but differ in their form and large size. The wolf does not "spread" the digits in the track, but holds the pads, as hunters say, more "balled up". The print of the anterior pads of a large central Russian wolf reaches 123 mm in length and 55 mm in breadth. The track of one wolf in the Priozern region of Arkhangel'sk district had a length of 130 mm and a breadth of 97 mm. The track of a huge animal, killed in Vladimirsk district in 1953, was 15 × 12 cm in shallow freshly fallen snow (N.D. Sysoev). The largest

*Literally *chernotropa*, or "black path;" see p. 242—Sci. Ed.

track of the anterior pad of a tundra wolf is 126×92 cm, and of the posterior, 123×80 mm (Timansk tundra; Semenov, 1954). The soles of the pads of the tundra wolf are better furred and the toes are more movable (expanding more widely). In tracks, females and males can be differentiated according to the manner of urination (the first is directly on the tracks, the second to the side). The she-wolf and the young leave their feces directly on the tracks, whereas the wolf usually moves aside from the tracks.

Trails of wolves differ from individual tracks in the somewhat larger size of the tracks, their compactness, the wider "drag"—the furrow in the snow, inscribed by the end of the wolf pad in the beginning of the step, and the "pillow case"—such a furrow at the end of the step (in front of the foot print).

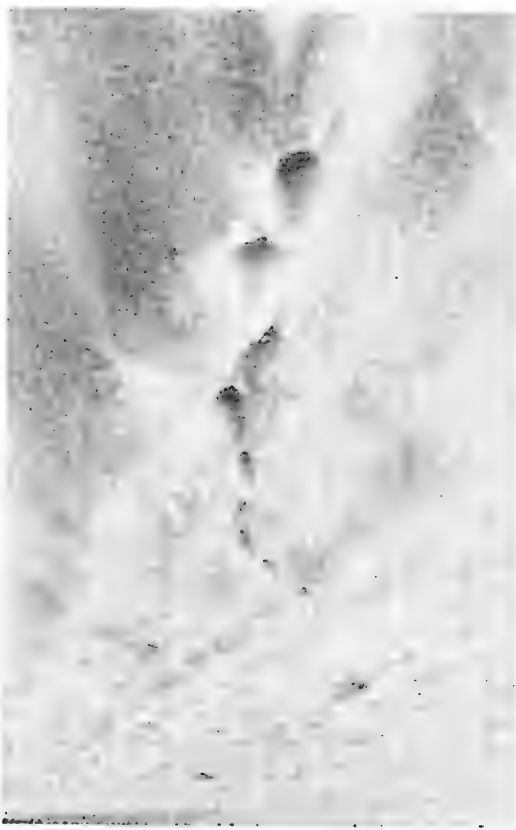


Fig. 72. Wolf trail. Track of four wolves proceeding "track in track". Khakassiya, Krasnoyarsk territory. December 1956. Photograph by V.V. Kozlov.

The voice of a mature wolf is a long bass howling. The male wolf gives voice through an octave, passing to a deep bass with stress on "O", and the she-wolf produces a modulated baritone through the nose, with stress on "U". Her voice is particularly mournful and wild. Yearlings howl with characteristic yelps resembling those of dogs. They include high notes and end by a characteristic barking. Juveniles almost never howl, but whine with laugh-like, thin voices. Howling wolves are heard for a distance of up to 2 km. The meaning of the howl is an assembly call for the mature wolves returning with prey and a signal of well-being in the region of the den. The male howls first, the female answers, and the young repeat in a dissonant chorus. Howling begins at twilight after sunset, and continues with pauses of usually not more than 15 minutes. Wolves do not answer a howl in rainy weather and when satiated (Danilov, 1945). In autumn and spring (until the birth of young), and sometimes in winter, wolves usually howl when going to hunt. In certain periods, for example, in the forests of the lower Samur river in southern Dagestan in August 1924, they "struck up a tune" with great precision at the coming of darkness (V.G. Heptner) (N.N.).

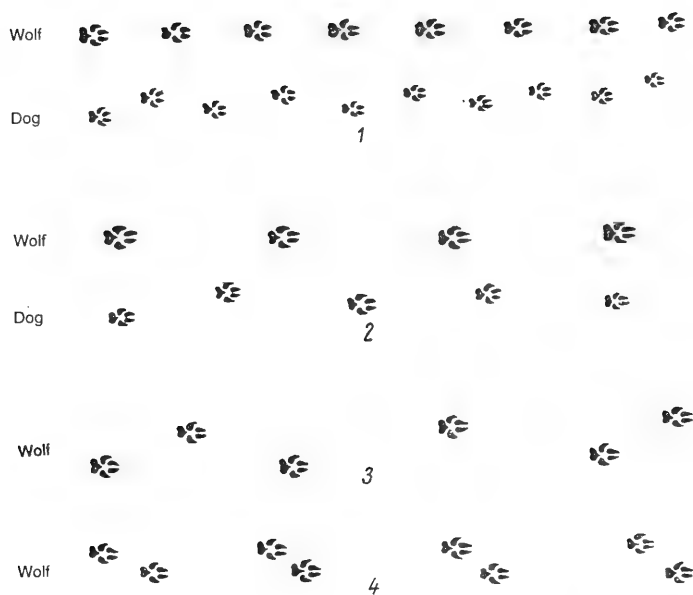
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Practical Significance

Wolves are harmful to humans in many respects: they attack livestock and dogs, wild ungulates and other useful animals, spread diseases and attack people directly. The little use which may be derived from captured wolves (skin, tasty meat which is fully suitable for food) as well as sporting pleasure of the hunting of wolves, are not to be compared with the damage to human health and economic interests caused by these undoubtedly injurious predators.

The average agricultural losses caused by wolves in the middle of the past century in only the 45 European governances of Russia were estimated at 179 thousand head of large horned livestock and 563 thousand of small annually, for a value of 7 million 600 thousand rubles in those day's prices (Lazarevskii, 1976). Animal husbandry in Vologodsk, Novgorodsk, Minsk, Volynsk, Kaluzhsk, Orlovsk, Ryazansk and Samarsk governances suffered especially from wolves. In 1871–1873, wolves killed an average of 2550 (0.29%) head of large horned livestock and 8550 (0.65%) of small livestock per year in Kiev governance alone. In Volynsk governance at that time, mortality reached 1.36% per year (12,300 head of large horned livestock and 19,600 of small; Korneev, 1950). Recently, the amount of harm sometimes

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188 Fig. 73. Scheme of tracks of wolf and dog in different paces of running (from Kozlov, 1955). 1—walking slowly, 2—trotting, 3—pacing, 4—galloping.



188 Fig. 74. Prints of front and hind feet of wolf on soft silt. Ganyshkino, in the delta of the Volga. 23 October 1951. Sketch by A.N. Formozov, about 1/2 natural size.

decreased and sometimes increased, growing particularly during social and economic shocks (wars, economic crises, crop failure and so on) as a result of weakening of predator control. This was noticed both with us, and abroad as well.

The harm caused by wolves greatly increased due to growth of their number after the First World War and then in the Civil War. In three republics: the Russian Federation, the Ukraine, and Uzbekistan—865 thousand head of livestock were registered as killed by predators in the agricultural year 1924/25, a sum of 15,530 thousand rubles in the price at that time. Approximately 35% of the losses took place in Siberia and Kazakhstan, followed by the other main stock-raising districts. In relation to all livestock in general, these losses consisted, in the lower Volga of 2.2%, in Siberia—1.6%, in Kazakhstan—1.5%, and for the whole territory of the USSR, 0.54% on average. Among the animals killed, 16% were horses (4.2% adults, 11.8% young), 18.1%—large horned livestock (6.8% adults, 11.3% young), 52.6%—sheep, 5.8%—goats and 7.2%—swine (Krasil'nikov, 1926). About 30% of the animals were killed in winter in the time of confinement in structures or in winter quarters. Many domestic poultry and dogs are killed by wolves. Hundreds of thousands of geese were exterminated yearly. In summer, they sometimes even comprised the principal food of wolves in a series of places. Although losses were reduced in 1928 due to the return of wolf control, until 1941 they remained in the vicinity of several hundred thousand head of livestock annually, i.e., quite high.

In connection with growth in the number of wolves at the time of the Great Patriotic War and afterward, there was a sharp increase in damage caused by them. Thus, in 1944 in the Buryat ASSR, more than 5300 head of livestock were destroyed by wolves; in Penzensk district, 780 horses and cattle, more than 5000 sheep, 300 swine and others were killed in 10 months of that year. Losses for the whole year approximated 8700 head of livestock in all districts. In Kuibyshevsk district, this figure reached 4200 head of livestock. In sheep-raising state farms, the wolves killed at that time 1–1.5% of the breeding flocks each year (Danilov, 1945). In Vornezh district, only the wolf population connected with Usmansk forest caused losses in the forest itself, and on 295 collective farms situated in its neighborhood, estimated at 760 thousand rubles in four years (1946–1949). During that time wolves killed on collective farms 164 calves, 163 foals, 3119 goats and sheep, 37 pigs, 3174 dogs, and 2500 geese. At that time as
190 well, in Usmansk forest wolves destroyed 200 deer and not less than

19 beavers (Martts, 1953; Barabash-Nikiforov, 1957). In 1946 in the Zyryanovsk and Asinovsk regions of Tomsk district, 600 head of livestock were slaughtered by wolves (Boikov, 1949).

The amount of damage caused by one litter of wolves can be judged by the fact that in Ryazansk district (Bel'kovsk region) 2 mature and 6 young wolves destroyed during 8 months (from May to December 1945) 6 horses, 1 foal, 5 cows, 150 sheep and goats, 3 pigs and many domestic geese, ducks and hens (Kozlov, 1955).

Annual losses to reindeer-breeding caused by wolves in the Yamalo-Nenetsk Nats. Region amounted to 1% of the population of the deer herds; in 1948, losses reached 2% (Rakhmanin, 1959). In 1951 they killed 1708, and scattered 7048 deer which "disappeared without a trace". In a decade (1944–1954) these losses amounted to about 75,000 deer (Semenov, 1954). In 1952 in Arkhangel'sk district, wolves and bears killed 1282 horses, 1343 head of large horned livestock, and 1806 sheep and goats. Of these losses, 64% took place in 7 southern regions of the district where wolves were especially numerous. Even greater damage to reindeer breeding was caused by wolves. Mortality of 3–7% of the domestic reindeer population was from wolves (Korsh, 1936). Losses of livestock due to wolves in Azerbaidzhan comprised 20–25% of the total losses in livestock breeding after the war (Vereshchagin, 1957).

These examples show how much the great losses after 1941–1945 were caused by the multiplication of wolves. To this must also be added the damage which is inflicted by wolves on dog husbandry by the destruction of hunting dogs during hunts, sometimes nearly in front of the hunter's eyes. Laikas and hounds in particular suffer from wolves, which follow their voices. However, wolves also attack watch-dogs, falling on them right in villages, or luring them beyond the outskirts.

Wolves cause great harm to the hunting economy, killing hares, foxes, game birds and waterfowl, wild ungulates, as well as muskrats, raccoon-dogs and even sables (Koryakov, 1947). Elimination of young wild pigs, red deer, roe deer, chamois and Kuban turs by wolves in the Caucasian preserve consisted in only 5 months of 34 to 61% (Teplov, 1938). In Il'mensk preserve, a litter of wolves in 180 days killed about 100 roe deer, or 15 animals per month on the average (S. Severtsov, 1941). In the lower Ili river, half of the roe deer and wild pigs born are killed by wolves in autumn. In years with deep snow, wolves may kill all of the young (Afnas'ev et al., 1953). In the winter of deep

snow in 1940/41 in Bashkir preserve, 35 roe deer were found killed by wolves, and in the winter of 1942/43, the remains of 8 bull and cow marals were met with (not all, of course, were found). A family of 7 wolves ate a whole bull maral during one night, leaving only shreds of the hide (Kirikov, 1952).

One wolf crossing ice to Barsa-Kel'mes island (Aral Sea) slaughtered 34 goitered gazelles and 1 saiga from March to June. Moreover, beginning in May, it ate the eggs and nestlings of gulls and caught sand susliks [*Spermophilus fulvus*] (Afanas'ev et al., 1953). Wolves cause particular harm to wild ungulates in the steppe and desert after calving, when they kill the young en masse (Heptner, 1956).

The intensification of wolf control in the post-war years sharply decreased the "wolf threat". However, it still continues to demand serious attention. Even though there is a relatively small number of predators, they are dangerous due to their boldness and bloodthirstiness. Attacking a rich quarry, for example a flock of sheep, the wolves kill much more than they need in order to eat. In December 1949, a wolf slaughtered 60 geese in one night on a poultry farm in Zhitomirsk district (Korneev, 1950). A litter of wolves, especially at the time of "hunting training" can kill 60–80 sheep in one flock (Sokolov, 1951).

191 In the autumn of 1920, on the headwaters of the Tobol in Kustanaisk district, wolves (probably a litter) on a dark night attacked a flock spending the night on the steppe, separated it from the shepherd and drove off the frightened sheep in the darkness, killing one after the other. In the morning, 52 carcasses were found on the steppe, lying in a long line in the direction of the flock's flight. Not far away, wolves attacked a herd of horses and slaughtered about 10 foals. All the animals were killed with a characteristic wolf bite—their throats were torn (V.G. Heptner). A wolf got into a sheepyard in winter in Redkovichi village (Belorussia) and killed 18 sheep in one night (Serzhanin, 1955). In June 1941 in the Izhevsk region of Ryazansk district, 2 mature wolves attacked a flock of sheep in a corral and in the course of one hour slaughtered 96 animals. On the night of 1 January 1950 in the Shilovsk region of Ryazansk district, 4 wolves got into a collective farm sheepfold and killed 78 sheep (Kozlov, 1955). At the end of June 1957 in Kopanov village in Ryazansk district, a wolf jumped over a wattle fence almost 2 meters high, and burst into a pen near the sheepfold where the sheep were driven at night. It killed and wounded 55 sheep, of which 5 in all were treatable. There was no watchman and the animal worked unhindered. Apparently, it did not carry off anything.



Fig. 75. Remains of saiga killed by a pair of wolves at a waterhole. Chu river valley, Kazakhstan. 3 November 1955. Photograph by A.A. Sludskii.

After this attack the pen was raised 70 cm and barbed wire stretched. After several days, the wolf reappeared and again penetrated the pen through a narrow space in the sheepfold wall where the barbed wire was not stretched. This time there were watchmen who raised an alarm, thereby giving the animal the possibility of a fortunate exit. It wounded 12 head in all of which 3 could be treated. In this way, the wolf destroyed in all 59 head in 2 nights (V.G. Heptner).

Wolves are the most dangerous vectors of rabies, not only because dogs and other animals (and recently, raccoon-dogs) are infected through them, but also because the bite of a rabid wolf is, in its consequences, about 15 times more dangerous than the rabid dog (Rudnev, 1950). Moreover, wolves serve as important vectors of helminths for domestic animals. The role of wolves in the transmission of the causative agent of "sheep gid[diness]" (*Multiceps multiceps*), and in part echinococcus, is of great importance.

Finally, even healthy wolves, although in very rare cases it is true, attack humans. More or less verified cases of attacks by healthy (not rabid) wolves on people have been registered in Belorussia (Serzhanin,

1955), in Kirovsk and Irkutsk districts (Timofeev, 1949), in the Kareliya (Marvin, 1959), and in the Ukraine (Korneev, 1950). All of them took place in winter, the time in which wolves are hungry.

Thus, in December 1947 in the vicinity of Suna station on the Kirov railway, a large man-eating wolf prowled about for one month. It usually went out around the village in the morning and evening, caught dogs and attacked solitary people, in daytime lying in the bushes near the road, not far from the village. In the course of one month, this wolf attacked people about 15 times. It bit and scratched 13 people, and tore to death two others (a woman and an adolescent). Killed after some time this wolf was found to be a large old male (head-body length 138 cm) that was extraordinarily emaciated. Except for a bundle of woman's hair, nothing was found in its stomach. Apparently, this wolf became a man-eater, being unable to catch ungulates. This was aided by the fact that during the war, eating of corpses by wolves was a frequent occurrence (Marvin, 1959).

In Ukraine, cases have been described when wolves attacked women in Dnepropetrovsk district in the winter of 1923/24 (Barabash-Nikiforov, 1928); two cases were registered in Stanislavsk district, one in Chernigovsk (attack on a shepherd in August), one—in Kamenets-Podol'sk and one—in Poltavsk district, when wolves killed three children (Korneev, 1950).

Control of wolves is carried out in various places by different means. Universally distributed are: a) extermination of litters in spring and summer in dens, when the pups are not yet grown and do not participate in hunting with their parents; b) capture of wolves with traps, especially in winter; c) application of poisoned baits. Traps are placed in trails ("under the track" or "in the track"), by lures, on scent trails, and near the so-called "urination points" (see above). Besides poisons which kill the animals (strychnine and others), soporific means (for example luminal) have now begun to be used by placing them in baits.

In the forest and forest-steppe zones in the second half of summer, autumn, and winter, they are hunted with an enclosure or by driving with or without application of flags. Hunting wolves with guns ("when howling") is successful. Near baits, and in summer also near the den, they stand watch with their guns. In the forest and forest steppe, *borzois* and hound dogs are used; in the east they are hunted with golden eagles, and sometimes the hunters bring wolves to bay on horseback. This method was particularly widespread in Kazakhstan. For this were

required the best (“*baigov*”)* horses, although wolves do not have great endurance when galloping. At full gallop, the animal is killed by a blow to the head with a heavy whip (*kamchi*).

For this hunting the Ural and Orenburg Kazakhs employed a long stick with a root-like knob on the *komi**. On such an “ukryuk” [lasso], a loop is usually fixed for catching horses from the herd. This method, to some extent, takes on a sporting character; however, capturing in this way was in the past one of the chief, if not the only method in the steppe, and in part, in the forest-steppe habitats of Kazakhstan (V.G. Heptner).

Self-snaring of wolves (loops, frames, cages, pits) are not efficient and have local significance; in the Buryatsk ASSR through self-snaring, 60 wolves were caught in 1946 (Manteifel’ and Larin, 1949). In Armenia, wolves are caught in winter in the unfrozen irrigation canals with quick current and cement walls by building a false bridge (Dal’, 1954).

The significance of these methods of exterminating wolves is not
 193 equal. According to data derived from a competition on the best means of extermination of wolves in 1927, the largest number of predators was caught by thorough extermination of litters in dens in summer (9.6–5.6 wolves per hunter); in second place was control by poisons (7.3–4.7 wolves per hunter); third—driving on horses (5.5 wolves per hunter); fourth—capturing with traps (4–3 wolves per hunter); fifth—capturing with dogs (3 wolves per hunter); sixth—by shooting from ambush near carrion (from 2.7 to 4.7 wolves); and seventh—drives using small flags (from 1.4 to 5.2 wolves) (Fedosov, 1939; Danilov, 1945).

In 1946, 263 wolf cubs were destroyed in dens in the steppe regions of Ryazansk district alone, in Voronezh—265, and 637 cubs in Astrakhansk. One hunter in Kirovsk district in the summer of 1950 exterminated 38 wolves by shooting them “when howling”; another got 17 wolves in this manner in 1949 and in 1950—36 wolves. With a golden eagle, one hunter caught in 1938/39, 154 foxes and 9 wolves, and another, in 1952/1953, caught 124 foxes and 26 wolves.

During the last few years, in open landscapes (tundra, forest-tundra, forest-steppe, steppe, desert) and even in the forest zone, the method of extermination from airplanes and airsled is found widely applied. In the winter of 1945/46 in Kuibyshevsk district, one pilot cornered and

*Turkic (?) word—Sci. Ed.

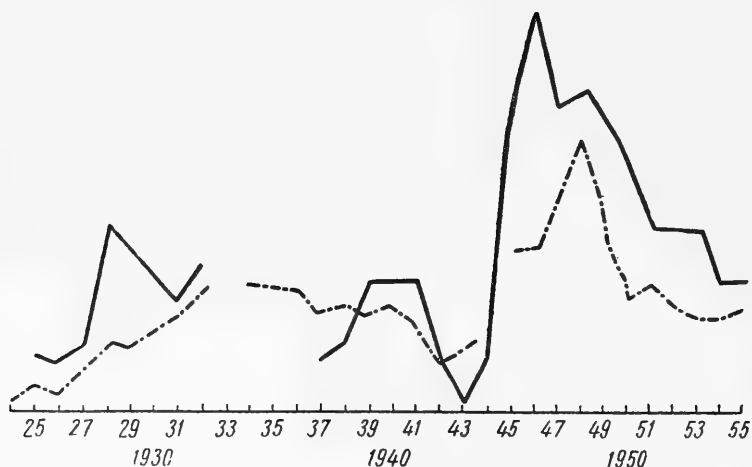


Fig. 76. Graph of tanned wolf hides as an indication of change in wolf numbers in the Caucasus by year. Continuous line—Cis-Caucasus; broken line—Trans-Caucasus (from Vereshchagin, 1959).

destroyed 180 wolves. Two pilots in the winter of 1947/48 killed 264 wolves from a PO-2 airplane in Tatariya and Chuvashiya (Popov and Lukin, 1949); in Kalininsk district, in the same winter, 200 wolves were caught from a PO-2 airplane (Kozlov, 1955). In March 1949, in Volgogradsk district, 38 wolves were killed from two airplanes in 7 days. In the Nenetsk Nats. Region, up to 1955, the average yearly number of wolves captured by all methods was 57 head (including cubs), a fact that restrained the growth in the number of wolves but did not decrease it. After employment of airplanes, the number of captured wolves grew sharply and the number of wolves and damage from them were reduced. Thus in 1955, 92 predators were killed by airplanes while all land-based hunters caught only 72 wolves; in 1956, 72 wolves were taken from airplanes, and 48 by land-based hunters (Makridin, 1959).

The wolves are very successfully driven and killed by airsled. It is applied in combination with an airplane (for reconnaissance) and airsled in radio contact sent by orders from the airplane for destruction of the wolf packs thus found (N.N).

Genus of Arctic Foxes

Genus *Alopex* Kaup, 1829

1829. *Alopex*. Kaup, Skizz d. europ. Thierwelt, I, p. 83, 85. *Canis lagopus* Linnaeus.

1868. *Leucocyon*. Gray. Proc. Zool. Soc. London, p. 521. *Canis lagopus* Linnaeus (V.H.).

Forms of moderate size.

Skull fairly compact with relatively narrowly placed zygomatic arches, quite massive and moderately high (height of the occipital region comprises about $\frac{1}{3}$ the condylobasal length). Sculpturing of skull, particularly sagittal crest, weakly developed, but greater than in g[enus] *Vulpes*. Facial portions moderately elongated (relatively shorter than in foxes of g[enus] *Vulpes*), quite massive but weaker than in the representatives of g[enus] *Canis*. Distance from line connecting the ends of supraorbital processes to anterior end of premaxillae longer than that to upper edge of occipital crest. Interorbital (frontal) area convex, somewhat elevated in area of frontal sinuses and, on the whole, noticeably and quite abruptly elevated above line of upper rostral profile. Supraorbital processes quite weak, flat or even slightly concave from above with tapering tip which is directed slightly downwards. Posterior edge of tooth row extends to level of anterior border of interpterygoid notch. Deep indentation and protuberance on lower edge of lower jaw in front of angular process absent.

Dental formula $I \frac{3}{3}; C \frac{1}{1}; P \frac{4}{4}; M \frac{2}{3}; = 42$. Teeth comparatively

moderate in size and massiveness, carnassial well developed; length of upper carnassial and cheek teeth goes into palatal length about $2\frac{3}{4}$ times. Canines quite massive, markedly curved and of moderate length (when the jaw is closed, tips of upper canines extend to the middle depth of mandible, while tips of lower canines reach alveoli of upper). Tips of upper canines directed straight downward; no distinct longitudinal cutting ridge on posterior side of canine and lateral surface of canine smooth. Incisors have no supplemental cusps, or they are very weakly developed.

Body notably elongated, tail quite long—about half the body length, ending considerably below the tarsal joint, and in standing animals reaching the ground. Head elongated. Ears long with rounded tip. On the soles of the

hind feet there are only 4 digital pads—behind them there is no large fifth pad.

The fur is very dense, luxuriant, long and soft. Winter fur is monotone and dimorphic—white, or more rarely grayish-brown; summer fur is dark in color with light flecks. There are two molts per year.

Supracaudal* gland not developed. From 5 to 8 pairs of teats (A.F. Shirkova)¹. Evident sexual dimorphism is absent; age is well marked, and seasonal dimorphism is very sharp, not only in the degree of density and length of fur but also in color.

Forms of the genus possess a quite typical foxy appearance.

They are inhabitants of the tundra and the Arctic islands. They accomplish regular seasonal migrations. They are monogamous, uniting together in the reproductive season. Up to 18 offspring (perhaps up to 20–22—the maximal number in the family and order), but usually less. The young are born only in a burrow. They are predators, feeding on 196 birds and small mammals (rodents), flotsam, and carrion. Apart from the breeding period, they pursue a solitary way of life.

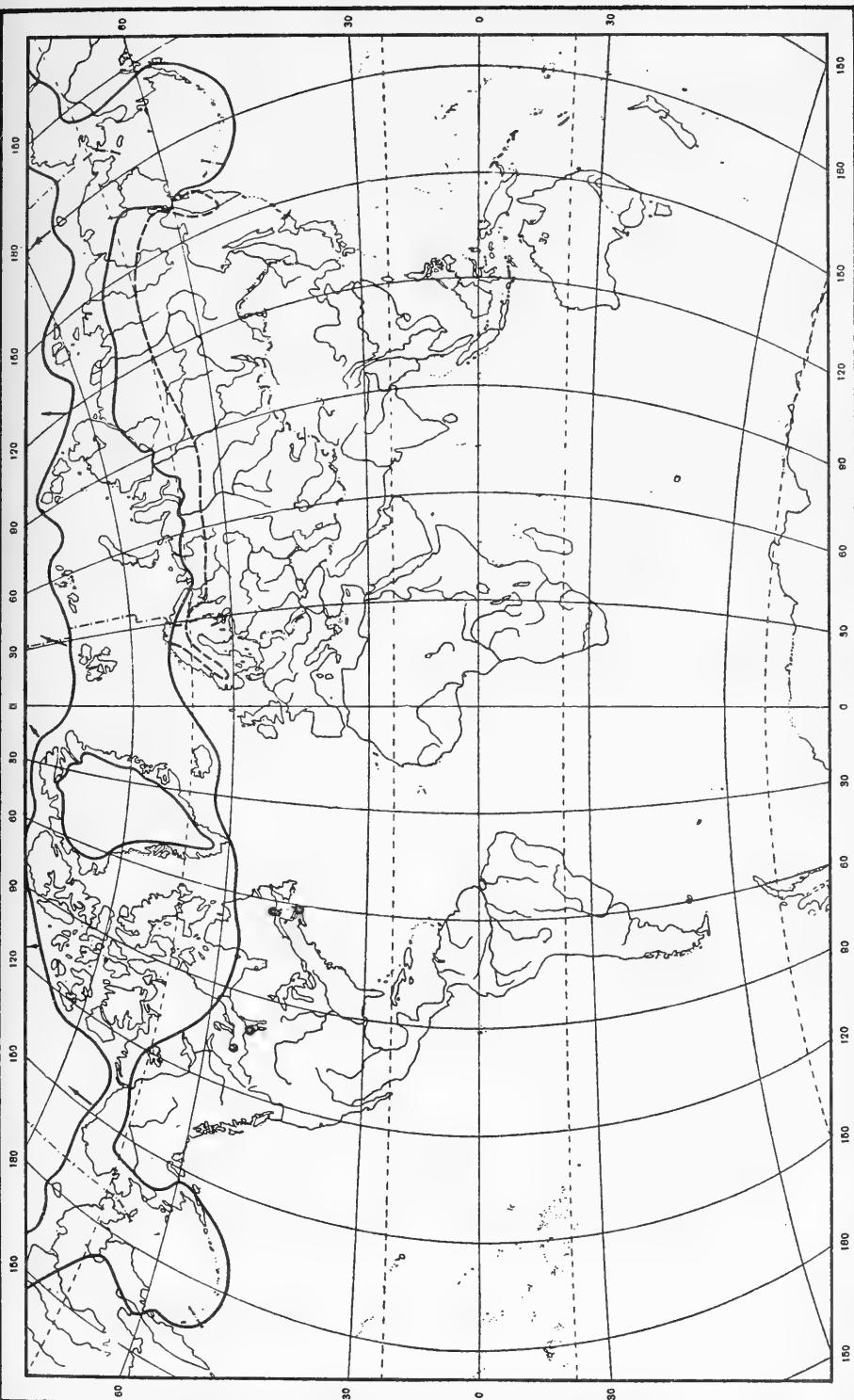
The range of the genus is remarkable in that it consists of two parts. One of these represents the region of reproduction and is occupied by the animals in summer time; the other is an area of transience and wintering, which they occupy in winter. The region of reproduction occupies the whole zone of tundra and the Arctic islands in the Old as well as the New World. The region of wintering and winter migrations extends on the north to the ice of the Arctic Ocean, and on the south to the region of stunted trees [*krummholz*] and the northern part of the forest zone².

Morphologically, the genus is somewhat less specialized than *Vulpes*. Physiologically, as typical arctic [forms], this group is very sharply specialized. The genus stands as a quite well-defined intermediate group between the genera *Canis* (wolves) and *Vulpes* (foxes). In some respects, it is closer to *Vulpes* and has been considered only a subgenus of the latter, although it has enough characters that ally it to the genus *Canis* also. More than anything, on the basis of the “intermediate”

*“Violaceous” in Russian original—Sci. Ed.

¹Reference to 6 (3 pairs) of mammae in the arctic fox, widespread in foreign literature, is incorrect. Such a number of mammae is not possible in an animal which gives birth to more than 10–12 young.

²Mammals migrating in a definite season from a more or less considerable part of their breeding range are very few. Cases in which the species leaves almost all its range are exceptional for the terrestrial mammals if some bats are not considered. Such type of migration is quite analogous to the migration of some birds.



195 Fig. 77. The range of the genus of arctic foxes, *Alopex* Kaup and the species range of the arctic fox *Alopex lagopus* L. in the Old World: solid line—boundaries of summer occurrence (denning), broken line—southern boundary of migration in winter. Points indicate places of individual particularly distant migrations to the south in the New World; arrows—the main directions of winter migrations to the north on the ice of the Arctic Ocean. Reconstructed range. V.G. Heptner.

characteristics of the genus *Alopex*, one may unite all three genera into one and consider them as subgenera. It has been assumed that *Alopex* is a subgenus of this broader genus *Canis*, which includes other groups besides the three already named (see above, characteristics of the family and of the genus *Canis*). At present, however, the majority of the authors consider the group *Alopex* as an independent genus. Until there is a more detailed analysis of the family system as a whole, this point of view is accepted here.

The genus is known from the Pleistocene (Europe), but it was, apparently, established in the upper Pliocene.

During the period of narrow interpretation of the species, some species were accepted into the genus (some authors considered up to 5 of them). It is now certain that the genus comprises only one species which constitutes about 3.5% of the species of the family.

In the fauna of the USSR, there is one species, *Alopex lagopus* Linnaeus, 1758; constituting 0.3% of the total species number of the fauna.

Its distribution in the USSR covers the tundra and northern islands from the Kola peninsula to Cape Chelyuskin and the Commander Islands.

This genus is one of the most important fur-bearing species in the USSR (V.H.).

ARCTIC FOX [POLAR FOX, PESETS]

Alopex lagopus Linnaeus, 1758

- 1758. *Canis lagopus* Linnaeus. Syst. Nat., Ed. X, 1, p. 40. Lapland.
- 1898. *Alopex lagopus spitzbergenensis*. Barret-Hamilton et Bonhote. Ann. Mag. Nat. Hist., 1, p. 287. Spitsbergen.
- 1902. *Alopex lagopus beringensis*. Merriam. Proc. Zool. Soc. Wash., 15, p. 171. Bering Island, Commander Islands.
- 1912. *Vulpes lagopus beringianus*³. Suvorov. Commander Islands and fur industry on them. p. 217. Commander Islands.
- 1931. *Alopex beringensis semenovi*. Ognev. Zveri Vost. Evropy i Sev. Azii [Animals of Eastern Europe and Northern Asia], vol. 11, p. 265. Mednyi Island, Commander Islands (V.H.).

³This transcription is sometimes wrongly ascribed to Cherskii, 1920 (Ellerman and Morrison Scott, 1951).

Diagnosis

The only species of the genus.

Description

In general appearance, the arctic fox is very similar to the common fox (*Vulpes vulpes*). In its short summer fur, it appears to have relatively longer limbs than the fox, with a shorter body. In its luxuriant winter fur, it seems to be more squat, although not so extended. The head of the animal in its winter fur is fairly rounded, with a somewhat blunt face and very widely separated ears which appear slightly above the fur; the ear tips are rounded. In summer fur, the head looks disproportionately large, with large and widely separated ears. The tail is long, about half the body length and, in winter fur is covered with long and luxuriant, extraordinarily dense hairs. When the animal is standing, the tail reaches the ground. The soles of the feet are covered with dense and long hairs, foot pads are not visible.

The summer fur is dense, soft and delicate, but short. The general tone on the back and neck is smoky-grayish-brown, sometimes with a mixture of reddish tones, that on the side is the same but with a lighter tone which passes to whitish on the belly. The thighs have the color of the sides and the legs, including the feet, are covered with brownish-gray fur. The dark color of the back in the region of the shoulder blades descends like a cape to the limbs and thus forms a cross-shaped figure

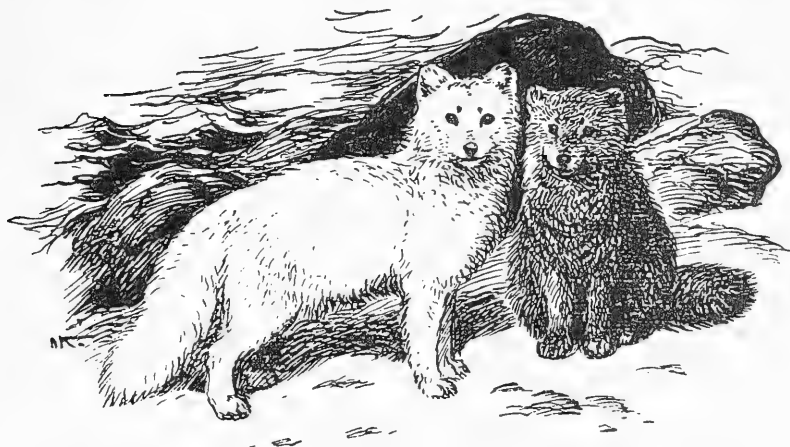


Fig. 78. Arctic foxes, *Alopex lagopus* L.—white (left) and blue. Sketch by A.N. Komarov.

(the summer Arctic fox is called “cross-fox”). The inner parts of the limbs are brighter than the outer. The tail above is brownish-gray, and the remainder is lighter, mixed with some pale-reddish-brown tints. The head is brownish-gray, the dorsal side of the ears is gray-brown and their front and inner parts are white.

The winter fur is extraordinarily long, dense, luxuriant and soft. The long and soft guard hairs form a beautiful “veil” of fur, and the very firm and dense underfur are characteristic. The color is entirely snow white, only sometimes with hardly noticeable creamy tints. In addition to this normal white color phase characteristic of the great majority of the animals throughout the entire range with the exception of some insignificant points, there is also a dark phase, called “blue fox”. The color of animals of this phase is very variable and varies from sandy, gray and light coffee-color to dark ash-gray with bluish tint; light and dark chestnut also occur, often with a more or less well distinct silveriness (white guard hairs). The whole body is of one color. The summer fur of arctic foxes of the dark phase does not differ, or only slightly differs, from the winter. The summer fur is of one tone and the “*krestovatik*” [“cross”] pattern* does not occur.

Sexual differences in color are absent, while age-related ones are quite considerable. New-borns are covered with short velvety fur of dark-brown color, only very slightly lighter on the sides. With age the lightening of color on the sides becomes stronger and gradually form the figure in the summer fur described above, and the little one leaves the burrow in a “young *krestovatik*” pattern*.

For characteristics of the skull and dental system, see above in description of the genus.

The diploid number of chromosomes is 54.

The size of arctic foxes is subject to quite considerable individual variation. Moreover, the average size of individuals of one population may vary annually. Extreme and average weights of the animals of one and the same population in different years may differ very greatly, depending on food reserves which annually change very sharply, perhaps being entirely different. Besides, the nutrient status of animals differs at different times in winter—the highest weight is in the beginning of winter, and by spring it strongly declines. In a good year, weight may increase even up to December, and its decrease begins with January. There is also geographic variation in size.

*See above—Sci. Ed.

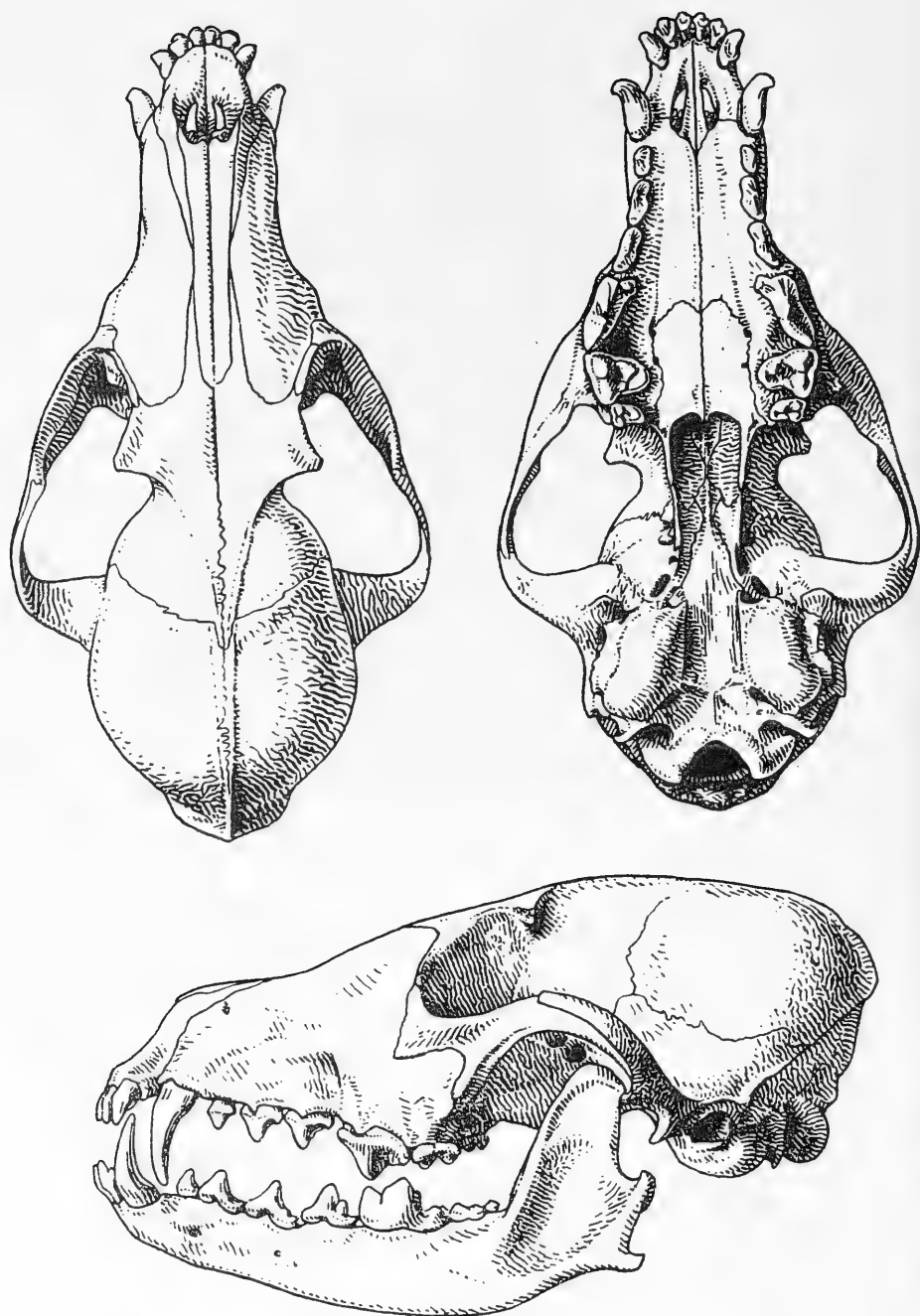


Fig. 79. Blue fox, Bering Island, October 1958. Photograph by S.V. Marakov.

Body length, 46.5–73 cm, tail length 25–52 cm. Weight changes from 2 to 8.8 kg (combined data of mainland and island animals, including Commander arctic foxes, but without Spitsbergen; see beyond, “Geographic Variation”). In the Lena delta in winter (November–March) 1935/36, weight of males (118) was 2400–6800 g, an average of 3816 ± 109 g; that of females (114) was 1200–5600 g, average 3091 ± 107 g; for the whole population the extreme variants (232) were 1200–6800 g, average 3453 ± 55 g. In Table 19, changes in weight in various months are given (Tavrovskii, 1939).

Greatest length of skull in males is 127–144.3 mm; in females, 119–136 mm; condylobasal length of skull in males is 114–138.5; in females, 111.0–127.2; zygomatic width in males is 64.7–78 mm; in females, 63.2–77.0 mm; length of upper tooth row in males is

*Omitted in Russian original—Sci. Ed.



53.1–61.3 mm; in females, 50.4–59 mm (skull dimensions include arctic foxes of the Commander Islands, but exclude Spitsbergen) (V.H.).

200 **Table 19. Weight of foxes in the Lena delta by months (in g[rams])**

Months	Males ³			Females		
	Minimum	Maximum	Average	Minimum	Maximum	Average
November	2400	5600	3753	1200	4600	3129
December	2700	5400	4036	2220	5600	3500
January	2500	6800	4012	2000	4400	2989
February	3000	4400	3607	2400	3700	2988
March	2450	3200	2850	1900	3000	2350

Systematic Position

The only species of the genus.

Geographic Distribution

The extreme north of Eurasia and North America. The borders of the range change considerably seasonally—the region of reproduction occupies the tundra and the Arctic islands, in the period of winter migration, it covers the northern part of the forest zone and the ice of the southern Arctic ocean. The region of irregular winter migrations of individual animals extends still farther, both to the north and to the south.

Geographic Range in the Soviet Union

This comprises a great part of the range of the species. Within the borders of our country is to be found in nearly all the Eurasian region of occurrence of the species. It occupies a relatively small part of the State territory on its northern frontier.

The southern boundary of the region of summer occurrence and regular reproduction in general follows fairly closely the southern boundary of the tundra, but in places, this strict coincidence is somewhat disturbed. On the Kola peninsula, the above-mentioned boundary

³It is significant that through January inclusively, the amplitude of weight fluctuations is very high—the smallest individuals are more than two times lighter than the heaviest. In the second half of winter, this contrast is less. Apparently, this takes place, to a certain extent, as a result of the decrease in the difference between young and old animals at the end of the winter (V.H.).

proceeds from Varanger Fiord, a little north of Murmansk, to the mouth of the Ponoï on the eastern shore of the peninsula. In places, the arctic foxes, under the suitable conditions (montane tundra), den somewhat to the south of this line.

On the eastern coast of the White Sea, the border passes a little to the north of the mouth of the Mezen', extends across Malozemel'sk tundra, mainly its maritime parts, and the northern part of the Timansk mountain chain. Crossing the extreme lower Pechora, the border goes farther to the east, along the watershed and the upper reaches of the Bol'shezemel'sk tundra rivers, i.e. along its middle and southern parts. At the Urals, the border extends nearly to the Arctic Circle or a bit north of it. On the Urals, the border descends to the south along the montane tundras.*

To the east, the boundary line slightly ascends to the north, reaching the mouths of Shchuch' and Ob', encircling Salekhard to the north and reaches the mouths of Nadym and Pur. Along the divide of the Pur and Taz, it descends quite a considerable distance to the south to the Arctic Circle. Farther to the east, the border passes northward along the right bank of the Taz beyond the Arctic Circle, crosses the Yenisei at the level of Noril'sk lake, includes them, and along the mountainous places (Putorana mountains?), makes an extension southward, including the sources of the Kureika and Kotue, and apparently Lake Essei, not reaching south, however, to the Arctic Circle.

201 From the above-mentioned place, the boundary rises quite abruptly to the north, crossing the Khatanga in its lower course and proceeding to the north of 70° N. Lat., crossing the Lena at its lowest reach. Farther on, it slightly descends towards the south, crossing at about 70° the Yana and Indigirka, and extending south of 70°, reaches the mouth of the Kolyma in the area of Nizhne-Kolymsk. From here, this line extends to the southeast, reaches the upper Anadyr', and thence abruptly turns to the south and even somewhat to the southwest towards Gizhiginsk gulf, thus becoming the western boundary for Chukotsko-Koryatsk part of the range. The southern border here, i.e. in the direction of Kamchatka, passes nearly along 60°, cutting across the very northern part of the peninsula. This is the southernmost known point of occurrence (denning) of the arctic fox.

With respect to information concerning the occurrence of the arctic fox in Kamchatka, they are contradictory. According to old data (Krashennnikov, 1762 and others), the arctic fox was encountered in

*Not evident on map, Fig. 81—Sci. Ed.

the entire peninsula or along its eastern coast to Cape Ukinsk (not far from Cape Kamchatka), and along the western coast—to its southern extremity (Cape Lopatka) or somewhat to its north. This information was interpreted by some authors as permanent occurrence, and by others, as winter migrations. In recent time there appeared a communication (Lavrov and Naumov, 1948), that a permanently occupied colony of arctic foxes is on the coast of the Sea of Okhotsk in the Ust'-Khairuzov region. All of this information is, for our time, either old or doubtful. One may think that the arctic fox is not present now in Kamchatka or it is extremely rare. In the past, it is apparent that, on the peninsula in the above-mentioned areas, transient animals (regularly migrating), were caught and farther south there were only rare irregular transgressions.

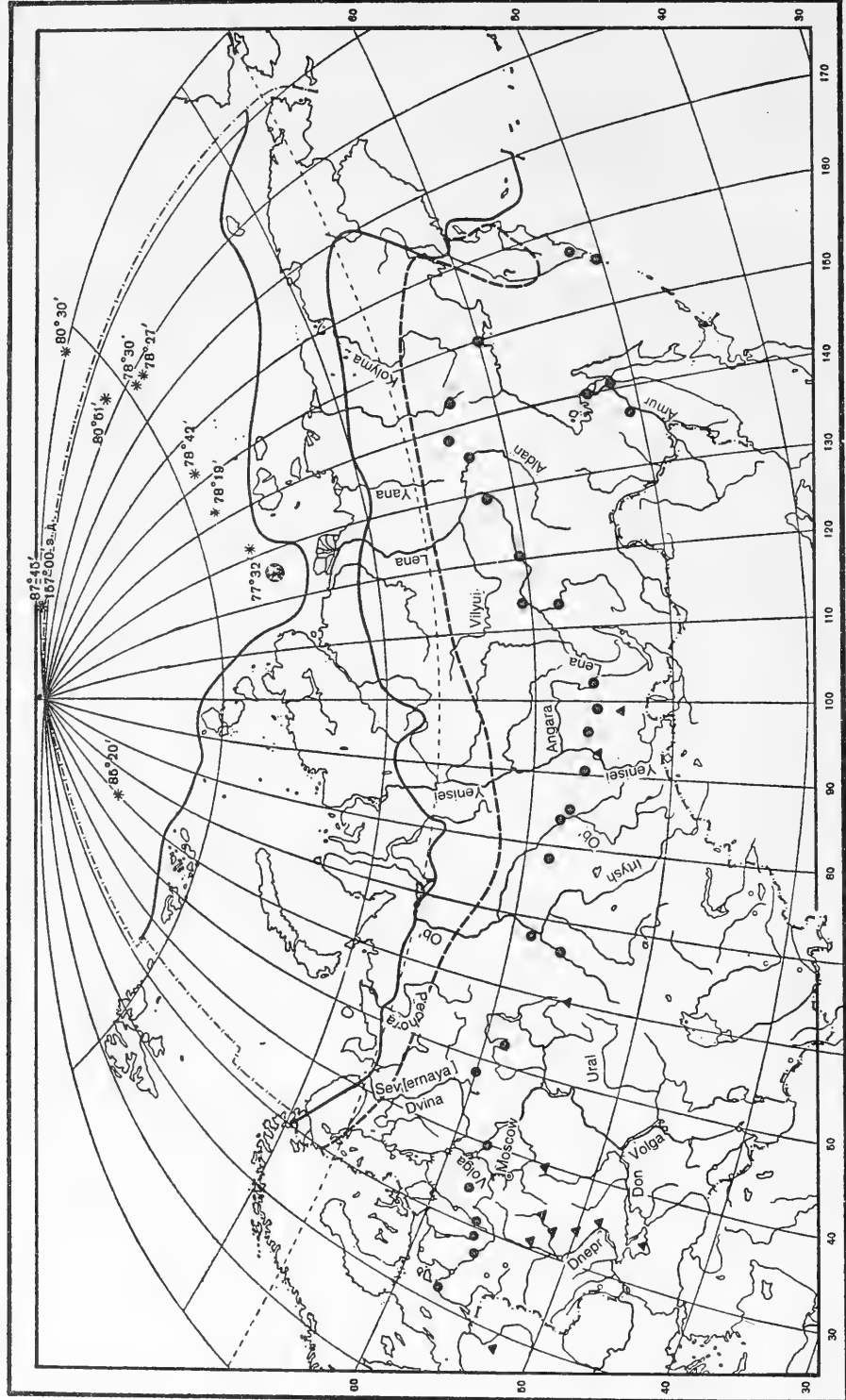
The northern border of the continental part of the range is everywhere formed by the ocean. Moreover, arctic foxes den in all the Arctic islands from Kolguev and Franz Josef Land to Wrangel' Island, and also on Kil'din on the Murmansk coast and on Karagin and Commander islands in the Bering Sea. Arctic foxes are absent only on several very small islands, lying in the open ocean, such as De Long Island. However, arctic foxes were found on Uedineniya Island in the Kara Sea (V.G. Heptner).

In spite of some old assertions, aboriginal arctic foxes are absent on the Kuril islands. In 1915–1916, blue foxes were brought from the Commander Islands to Ushishir (Usisira) Island where they survived well and reproduced. In the 20's and 30's, arctic foxes were brought to the islands of Simushir (Sinsiru), and from the small Kuril islands of Yuru (Yurii, Uriri), Kharukaru* and Lis'i (? , V.H.)**. On the Malyi [small] Kuril islands at the present time (60's) foxes are apparently absent (Kuznetsov, 1939; V.G. Voronov and A.G. Voronov).

The southern border of the area of regular migrations—the winter range—in the extreme west passes along the southern coast of the Kola peninsula. Within Kareliya, normal migrations are not common, and here only occasional long movements are known. The southern border of the above-mentioned area between the White Sea and the Urals traverses the northern part of the forest zone (V.I. Parovshchikov), i.e. somewhat south of the Arctic Circle, although not rarely the arctic fox also penetrates far to the south.

*Kharimkotan?—Sci. Ed.

**This query by Heptner is not explained, but may refer to the source(s) from which the above data are derived. In particular, the context of the sentence suggests that foxes were not brought from, but rather, to the small Kuril islands—Sci. Ed.



To the east, the boundary of winter habitation crosses the Urals and the Ob' somewhat to the south of 65°, reaching the upper Pur and Taz, or in the vicinity of their watersheds with Vakh, and crosses the Yenisei at Verkhne-Imbatsk (below the mouth of the Podkamennaya Tungus). Thereafter it goes to the source of the Vilyui and crosses the Lena, Yana and Indigirka rivers around the Arctic Circle or a bit more to the north, passes over the Kolyma slightly above Verkhne-Kolymsk (considerably south of the Arctic Circle) and, still descending southward, reaches the Penzhinsk Gulf. This district includes the northern and western (excepting the extreme south) parts of Kamchatka.

In general, it may be assumed that winter migrations of the arctic fox extend to the northern parts of the forest zone—sometimes quite deep into it. In such cases, apparently foxes of the extreme west (Kola peninsula) roam to the south least of all; there is comparatively little shifting of the range in the remaining European part of the [Soviet] Union and in Yakutiya, and animals in west and central Siberia move southward farthest of all. Evidently very distant migrations occur in places in northeastern Siberia and Kamchatka.

Migration of separate individuals does not always take place directly south- or northward. Many animals also move in other directions. In different regions, there may be different predominant directions. Thus, arctic foxes from Yamal move mainly to the southwest and straight west, going as far as Cheshsk Gulf. Animals during these journeys put behind them many hundreds, even more than a thousand, kilometers, without even leaving the region of summer distribution of the species. This probably explains the fact that in the European part of the [Soviet] Union, the border of the winter habitation of the arctic fox shifts comparatively little (for more see description of migrations in the section "Biology").

- 202 Fig. 81. The range of the arctic fox, *Alopex lagopus* L., in the USSR (reconstructed). The continuous line limits the southern region of summer habitation and reproduction (denning), the dashed line—the region of regular wintering and permanent winter migrations. Dots indicate places of most distant winter transgressions of separate individuals to the south, stars—to similar places to the north on the ice of the Arctic Ocean, figures near them give the latitude. The question mark in Kamchatka refers to the place (Ust'-Khairuzovo) regarding which there is information about the denning of a small group of animals in an isolated spot, triangles—places of Upper Pleistocene finds of arctic fox. V.G. Heptner.

The outlined southern boundary of the region of normal winter distribution is entirely tentative. The reason for this is above all an insufficiency of accurate materials. Moreover, this line is much less sharp in nature than the boundary of the area of denning. Depending on various reasons, in one and the same district, the distance of migration to the south and the number of animals coming from the north, may annually change noticeably. Therefore, the border may be situated in the south sometimes far and sometimes near, while at the same time, in various parts of the range, these annual variations may be expressed in various degrees. Finally, in a series of cases, with the presence of data in the literature, it may be difficult to decide whether, in a given place, we deal with regular residence of a small number of individuals, i.e. with the district of normal wintering, or with a place whence separate vagrant individuals migrate comparatively frequently, i.e. with a district of long-distance transgressions (in the present description, the southern boundary of the normal migration to the south is directed, apparently, somewhat more to the south than is accepted by some authors, at least for separate parts of the range).

To the south of the region of regular wintering is situated a wide zone of irregular transgression of separate vagrant individuals. They often transgress so far to the south, that they, apparently, do not have the possibility of returning back, and in the long run they probably die. The following most distant places of transgression are known (extreme points, from west to east, Fig. 81; for more see the section "Biology"): Baltic Sea coast at Ventspils (Vindavy; Van den Brink, 1958), Daugavpils on the Zapadnaya Dvina (about 56° N. Lat.), upper Velikaya river, flowing into Pskovsk lake, Velikie Luki region, northwest of Yaroslavl' (58° N. Lat.), northwest of Kirov at 60° N. Lat., the Omutninsk region in the upper Viatka at 58°40' N. Lat., northwest of Tobol'sk, approximately at 59° N. Lat., Yalutorovsk on the Tobol at 56°40' N. Lat., middle course of the Vasyugan—a tributary of the Ob', the mouth of the Parabel' at the Ob', Kolpashovo on the Ob' at 58°30' N. Lat., the Chulym river to the north of Achink (about 57° N. Lat.), Kansk (west of Krasnoyarsk), Taishet (west of Krasnoyarsk at 56° N. Lat.), Bratsk on the Angara, Cheremkhovo on the Angara (to the northwest of Irkutsk at approximately 53° N. Lat.); one of the southernmost points in Siberia), Bodaibo on the Vitim (about 58° N. Lat.), Mukhtui on the Lena (about 60° N. Lat.), Olekminsk on the Lena, Yakutsk, mouth of the Tompo river at the Aldan, source of the Tompo river (about 64° N. Lat.), Oimyakon

(about 63° N. Lat.). Tauisk Gulf on the Sea of Okhotsk, southern Kamchatka (about 52° N. Lat.), northern Kurils. Migrations to the lower Amur and Komsomol'sk-on-Amur—50° N. Lat. are known (points from personal material of A.F. Chirkova). It is possible that migrations to the lower Amur may be in part connected with the movement of animals along the ice or drifting with floating ice. Therefore, in the European part of the country migrations extend to 56° N. Lat., in the Asiatic—nearly to 50° N. Lat. This difference could be explained by the fact that conditions characteristic of arctic fox are, in Siberia, distributed farther to the south than in the west; in particular, montane tundra extends far to the south. Another reason
 204 is that human settlement in the west is much more dense and the animals die earlier, before they attain their natural movement.⁴

Winter outposts of arctic fox from the region of reproduction occur not only in the south, but also in the north—on the sea ice. Movement in this direction represents an entirely normal phenomenon, since in its wandering on the ice, the arctic fox usually follows the [polar] bear. It is evident that in southern latitudes and districts of the Arctic Ocean, this is a “regular” winter habitation to very distant places—“irregular long-distance transgressions.” However, the definition of these districts is still almost impossible.

As shown by observations in recent years, including both our own and also American drifting research stations, arctic foxes are more common in the region of the southern sea margin and southern parts of the Arctic Ocean, and the farther toward the polar district, the rarer they become. Known extreme points of arctic fox finds show that they penetrate to the most inaccessible parts of the Arctic Ocean farthest from land, and that they probably reach the pole. Very many cases of arctic fox observations are known from the ice region relatively close to the continent (up to 100–150 km). The following are the most northerly encounters in the waters in our sector of the Arctic: 77°32' N. Lat.—132°59' E. Long.; 78°19' N. Lat.—141°33' E. Long.; 78°27' N. Lat.—177° E. Long.⁵; 78°30' N. Lat.—176°03' E. Long.; 78°42' N. Lat.—152°33' E. Long.; 80°30' N. Lat.—159°50' W. Long.; 80°51' N. Lat.—176°00' W. Long.; 85°20' N. Lat.—about

⁴Information concerning the capture of an arctic fox in the Tien Shan, which is widely found in the literature (for example, Ognev, 1931), and even used for some historical formulations is based on a misunderstanding: the skin pertains to an albino red fox (Afanas'ev et al., 1953).

⁵“Pravda” newspaper on 16 April 1941.

60° E. Long. (our northernmost point; Chapskii, 1946; Rutilevskii, and Uspenskii, 1957).

All points mentioned are distant from the nearest land by several hundred kilometres—in a biological sense, this is more important than the latitude. Thus, the place of occurrence at 85°20' N. Lat. stands 550 km from Rudolf Island (Franz Josef Land); the point at 78°27' Lat. lies more than 500 km distant from De Long Island and more than 750 km from Wrangel Island; the point at 78°30' lies 750 km from the New Siberia[n Islands]; that at 80°51'—900 km from land; and the point 80°30' and 159°50' W. Long. found in the "pole of inaccessibility", is 1025 km from Point Barrow in Alaska and 1125 km from Wrangel Island. In the American sector of the Arctic, the arctic fox was noted at 87°, 460 km north of the northern tip of Greenland, and at 88° N. Lat., 800 km from Ellesmere Land.

In the Quaternary period, the arctic fox was distributed much farther to the south. Its Pleistocene remains are known in all countries of Western and Central Europe, including Ireland, southern France (Pyrenees), Switzerland, Czechoslovakia, and Poland. Within our boundaries, the remains of arctic foxes are known from the Gomel', Bryansk, Lipetsk, Chernigov, Poltava, Dnepropetrovsk regions, and even the Crimea. In the east, Pleistocene arctic foxes were found in the Chelyabinsk, Krasnoyarsk and Nizhneudinsk regions. Therefore, they could be found in the south as far as 44°40' N. Lat. (Crimea) and about 55° N. Lat. (Siberia). This demonstrates that contemporary transgressions of arctic fox, both in the European part of our country, and in the east (Pri-Baikaliya) reach or nearly reach the places of their Quaternary occurrence.⁶

205 It is remarkable that in spite of very ancient and very intensive exploitation, not considering the comparatively small territory of Kamchatka, the range of the arctic fox did not suffer any essential changes.

⁶Range according to data of Krasheninnikov, 1786; Maak, 1859; Middendorff, 1887; Pleske, 1887; Ognev, 1926, 1931; Solov'ev, 1927; V.N. Skalon, 1928; Formozov, 1927; Paramonov, 1929; Yakovlev, 1930; S.P. Naumov, 1931; N.P. Naumov, 1934; Tugarinov, Smirnov and Ivanov, 1934; Kolyushev, 1936; Heptner, 1937; Sdobnikov, 1940; Chapskii, 1946; Kuznetsov, 1949; S.P. Naumov and Lavrov, 1948; Stroganov, 1949; Shvarts, Pavlinin and Danilov, 1951; Yanushevich and Blagoveshchenskii, 1952; Lable, 1953; N.I. Dement'ev, 1955 and others, and according to unpublished materials of V.N. Skalon, V.Ya. Parovshchikov and V.G. Heptner.

For additional data concerning transgressions, see section on "Biology".

Geographic Range outside the Soviet Union

In Europe—the extreme north of Scandinavia and the highest parts of the mountains of the peninsula facing the Atlantic Ocean, as a narrow strip to the south, nearly to 60° N. Lat. In winter wanderings—all of Finland, and all Norway and Sweden to its extreme south. Apparently, they migrate onto the ice of the Baltic Sea. The islands of Spitsbergen, Jan Mayan, and Iceland.

In North America, the southern boundary of the range covers the northern parts of Labrador, the Ungava peninsula, and the district lying to the east of Hudson Bay. Across the bay and beginning on its western shore slightly south of 60° N. Lat., the boundary passes westward approximately along this parallel, south around Great Slave Lake and along the Mackenzie river to its delta. Farther on, it encompasses the northern and western parts of Alaska, reaching the ocean at Cook Inlet. To the north of this line, the range includes the entire northern periphery of the continent and all the islands of the American Arctic and all adjacent districts of Greenland. In the Bering Sea, the range includes the Aleutian and Pribilof Islands and Hall, Saint Matthew and Saint Lawrence islands. On winter migration, arctic foxes reach as far south as the Gulf of Saint Lawrence, and the northern parts of Alberta, Saskatchewan and Manitoba (i.e. approximately 55° N. Lat.). Particularly distant transgressions extend to 50° and even 45° N. Lat. (Nova Scotia). (V.H.).

Geographic Variation

Compared to the ranges of such species as the wolf or red fox, the range of the arctic fox is not great⁷. Moreover, it is distributed in one landscape-geographic zone, and in the various parts of the range there are no sharp contrasts in conditions of existence which may stimulate geographic variation as an adaptive process. Finally, the arctic fox is characterized by seasonal migrations, since some animals move for enormous distances, without leaving the region of habitation and reproduction of the species. This provides a high level of panmixia in the species population. Thanks to the continuous cover of arctic ice and the wide migrations of animals on the ice, island

⁷The exaggerated extent the dimensions of the range of the arctic fox is based on the wide use of maps with Mercator projection.

isolation is practically not met with. Within the boundaries of our country, it exists only in relation to the Commander islands, where a separate race was formed. In the parts of the range outside the USSR, the same conditions and the same tendency towards the formation of forms are generally revealed.

In our part of the range, the following subspecies are distinguished.

1. Continental arctic fox. *A. l. lagopus* Linnaeus, 1758.

Color of winter fur is snowy-white, of summer fur smoky-brownish-gray (see above); the dark phase is very rare and is usually encountered in the proportion 1 : 1000–2000. Changes in this ratio in different parts of the range are negligible. Only on Kil'din Island on Murmansk coast, the percentage of blue reached 30–50.

Skull^s of moderate dimensions, quite broad and high; muzzle relatively long (its length constitutes 43–48% of condylobasal length); interorbital region wide; infraorbital processes of moderate size; postorbital constriction not sharp; braincase quite high and wide—its height represents 36–43%, and width—34–41% of condylobasal length. Cranial crests not large, but well defined. Proximal ends of nasal bones located at the level of the upper borders of the frontal processes of the maxillary bones or somewhat beneath it, rarely higher.

Size not large; body length 45–70 cm, weight to 7 kg.

Greatest length of skull of males 127–136 mm, of females 119–131 mm; condylobasal length of skull of males 114–132 mm, of
 206 females 111–127 mm; zygomatic breadth of males 64.7–73.7, of females 63.2–70.3; length of upper tooth row of males 54.1–61.3, of females 50.4–59.0.

Continental part of the range, from the Kola peninsula to Chukotka land; all Arctic islands except, perhaps, Franz Josef Land.

Not recorded outside the borders of the USSR, but perhaps distributed in Alaska.

The Novaya Zemlya arctic fox were, in part provisionally, sometimes separated as *A. l. spitzbergensis*. This, however, is unfounded, for they cannot be differentiated from those of the continent by skull dimensions. The above-mentioned form is characterized by very small size (condylobasal length of skull 105–120 mm), and infantile skull type—the skull of adult Spitsbergen animals corresponds to that of

^sCharacteristics of the skull here and later after Tsalkin (1944). Dimensions of skull after Ognev (1931).

subadult continental ones. That the arctic foxes of the Franz Josef archipelago are related, or close to, the Spitsbergen form, is not excluded, however, nothing is known of them.

Craniologically, arctic foxes found in the whole of the above-mentioned expanse are identical; however, fur merchants differentiate here the following types (Kuznetsov, 1952).

Novaya Zemlya type. Skins of this type are differentiated by especially high quality. They are characterized by large dimensions (weight of 100 skins about 30 kg), luxurious silky pelage with tall, elastic guard hair and dense underfur, and by the snow-white color. Flesh side of skin compact.

Novaya Zemlya.

Yenisei type. Skin quality nearly equal to Novaya Zemlya and almost the same dimensions (100 hides weigh 28 kg). Pelage only slightly less silky.

Tundra between Taz and Anabara.

Yakutsk type. Skin dimensions slightly less than the former (weight of 100 hides 25.5 kg). Pelage characterized by fluffy, and chiefly, by exceptional silkiness; guard hair fine, delicate, less elastic and underfur dense. Color clear-white. Flesh side of skin thin.

Yakutsk tundra.

Obdorsk type. Skins of moderate size (weight of 100 hides less than 27 kg). Pelage not so fluffy and markedly less silky than that of preceding types, with short, especially on the back, elastic guard hair

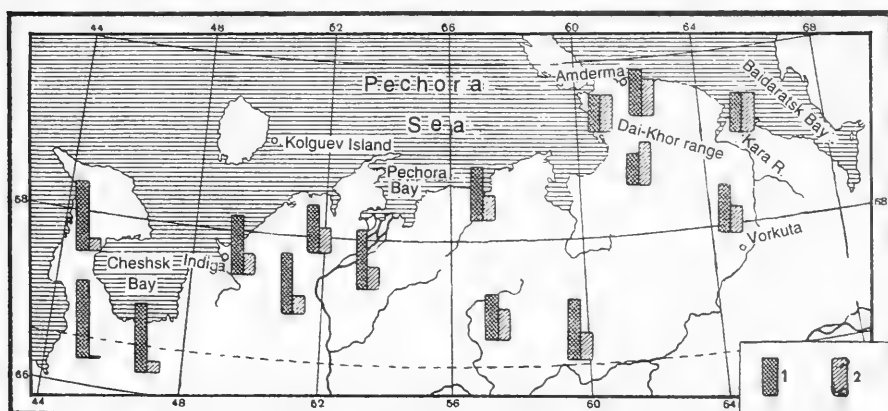


Fig. 82. Ratio of fur types in tanned skins of white arctic fox in tundras of Arkhangel'sk district in the year of movement of arctic fox from the east (of 100% at each point) (A.F. Chirkova): 1—Pechora type, characteristic of European North; 2—Obdorsk type, characteristic of Yamal.

and dense underfur. Color white, but usually with light creamy tone. Flesh side of skin compact.

Region between the Urals and Taz.

Pechora type. Skin dimensions small (100 hides weigh 26 kg).

- 207 Pelage less fluffy, with short guard hair and loose underfur. Color white, with barely noticeable bluish tone (color of skimmed milk). Flesh side of skin compact.

Tundras of the European part of [Soviet] Union.

2. Beringian arctic fox, *A. l. beringensis* Merriam, 1902.

Color of winter fur light or dark-brownish, usually with more or less well-defined silvery highlights. Dark smoky skins with deep bluish underfur ("dark blue") are relatively scarce. Fur is extremely fluffy, but somewhat coarse, with well-developed guard hair. White color phase is absent or found in the form of extremely rare individual cases.⁹

Compared to skull of continental arctic fox, skull narrower in region of zygoma and braincase, its height less, supraorbital processes and postorbital constriction more sharply defined, teeth larger, crests more strongly developed.

Measurements are somewhat larger than continental ones. Body length of males 46–67, average 60 cm, females 41–64, average 57 cm; weight of males is 3.5–8.8, average 5.5 kg, females 2.5–6.4, average, 4.4 kg.

Condylobasal length of skull of males 121–139 mm, females 116–134 mm. Length of nasal bones in males 41–57 mm, females 41–50 mm.

Bering Island.

Absent outside the borders of USSR.

3. Mednyi [Copper Island] arctic fox, *A. l. semenovi* Ognev, 1931.

Color of winter fur of the majority of animals is dark-brownish without admixture of white and silvery hairs. Clear-gray ("blue") arctic foxes occur in comparatively small numbers. Fur is somewhat coarse, with weak, scattered guard hair. White color phase is absent or is found in the form of extremely rare individual cases.¹⁰

⁹Characteristics of color and fur, and general dimensions of this and following forms mainly after Kuznetsov (1952).

¹⁰In the past, with suppression of the predominate dark color phase, as on both Mednyi island and on Bering island, white arctic foxes were met with more often than in the present time. The present situation is the result of the deliberate elimination of the white forms over the course of many decades.

Skull noticeably larger than that of continental arctic fox, narrow in zygoma and in region of braincase, its height less, nasal bones shorter, supraorbital processes and postorbital constriction more sharply defined, teeth stronger. Skull crests, especially lambdoidal and region of interparietal bone are very robust—much more robust than in continental animals.

Dimensions considerably larger than in continental arctic fox, and somewhat larger than in Beringian one. Body length of males 61–73, average 68 cm, females 60–68, average 64 cm. Weight of males 4–8.8, average 7.2 kg, females 4–7.2, average 6 kg.

Greatest length of skull of males 130–144.3, females 122.6–130; condylobasal length of skull of males 116–139 mm, females 116–131 mm; zygomatic width of males 72–78 mm, females 66–77 mm; length of nasal bones of males 36–45 mm, females 34–44 mm.

Mednyi [Copper] Island.

Absent outside the boundaries of USSR.

Bering and Mednyi arctic foxes are extremely close to one another, although the differences between them are quite real. Mednovsk are also distinguished from Beringian in averaging shorter nasal bones.

It is worth mentioning that, at the same time that European island races of arctic foxes (*spitzbergenensis*, *fuliginosus*) are quite regularly characterized by their small measurements and by some infantile features of skull structure, in Commander (Aleutian and Pribilof) arctic foxes, these are not observed. They, on the contrary, are larger than continental ones, with more specialized skulls (with features of 208 hypermorphosis). Probably, this is explained by the very favorable conditions of existence, in the sense of food supply, of arctic foxes on the above-mentioned islands.

For the part of the range lying outside our boundaries, the following subspecies are usually accepted.

1) *A. l. spitzbergenensis*—Barr.-Ham. et Bonh., 1898—Spitzbergen; 2) *A. l. fuliginosus* Bechst., 1799—Iceland; 3) *A. l. groenlandicus* Bechst., 1799—Greenland; 4) *A. l. ungava* Merr., 1884—Labrador and Ungava; 5) *A. l. innuitus* Merr., 1902—Continental tundras and islands of America, except the regions occupied by the forms *ungava* and *groenlandicus*; 6) *A. l. pribilofensis* Merr., 1902—Pribilof islands; 7) *A. l. halensis* Merr., 1900—Hall, Saint Lawrence and Saint Matthew islands in the Bering Sea.

Arctic foxes of the American islands—Pribilof and Aleutian, like the Commander islands, represent the dark phase. Apparently, not all

the listed forms are sufficiently well characterized and well grounded (V.H.).

Biology

Population. In the tundra zone of the USSR, the arctic fox is the most common and abundant carnivore, substituting here for the red fox.

The number of arctic fox is extremely unstable; it sharply changes by years and by seasons of the year. In autumn and at the beginning of winter, in some years, one may encounter tens and even more arctic foxes in the course of a day, and in other years, especially in spring, only a single individual in the course of a month.

For orientation, one may assume that the overall arctic fox population in the season before the beginning of harvest amounts, in the Soviet sector of the tundra zone, in different years, to from several tens of thousands to several hundreds of thousands¹¹. Arctic foxes are most abundant in the Bol'shezemel'sk, Yamal'sk, Prieniseisk, Prilensk and Ust'yansk tundras.

Arctic fox stocks are not great in the narrow belt of the Iokan'go-Ponoisk tundra on the Kola peninsula (see Table 20 and beyond). In the tundras of northern Arkhangel'sk district, the arctic fox inhabits most densely the northeastern Bol'shezemel'sk tundra. In some years, these tundras are full of arctic foxes migrating from the east. Arctic fox is quite abundant in the north of the Kanin peninsula (Table 21). In a year of small numbers of arctic foxes (winter 1951/52) in an area of 400 km², only 3 arctic foxes were taken in a drive; in a year of high numbers (winter 1953/54) in several drives on an area of 20 km², about 15–30 arctic foxes were taken in December, and in the second half of winter about 7–15 arctic foxes.

In the Malozemel'sk and Bol'shezemel'sk tundras during the time of land development work, the general number of burrows was revealed (Table 21), the density of which in the northern subzone of the tundras increased 3 times. The total number of arctic foxes was arrived at (Table 20) by an average "yield", by considering 30% of the holes as being occupied and by taking into account two pups for each breeding. In these tundras, 7 large "hearths" of reproduction of

¹¹Boitsov (1937), taking the area of tundra as 3,116,500 km², considered the number of arctic foxes in the 30's to be 100,000 breeding pairs. From this, each pair of animals inhabits, on the average, 31 km² or a population density equal to 1.3 per 1000 ha.

arctic foxes were discovered, with the density of burrows ranging from 2.9 to 5.6 per 1000 ha in each, and an average of 4.8. The area of the hearths comprises about 16% of the entire land of Malozemel'sk and Bol'shezemel'sk tundras, and includes about 27% of all discovered burrows (Skrobov, 1958). In the east of the Bol'shezemel'sk tundra, burrows are located at a distance of 1–2 km from each other, and rarely at a distance of 400–500 m (A.T. Voilochnikov, Yu.T. Nazarenko). At the mouth of the Pechora, in autumn 1944, with abundance of arctic foxes close to the multiyear average, hunters found in one harvest day 3–10 polar foxes, while in autumn 1954, with numbers negligible, 1–2 foxes in 10 days.

209 In winter 1956/57, on a route of more than 500 km in the region of Kara Bay at the extreme northeast of Bol'shezemel'sk tundra, for each 20 km of the journey, from 19 tracks in November to 1 track in January, averaging 2–6, were found. In winter 1957/58 in a year of diminished numbers of arctic foxes was recorded (on a route length 1500 km) an average of 0.7 tracks (Chirkova, 1955; Chirkova et al., 1959). The fox population in Novaya Zemlya was calculated to be several thousand head (Dubrovskii, 1937) (Table 20).

211 In Yamal, a great number of arctic foxes live in the northern subzones of the tundra (Dubrovskii, 1940; Freiberg, 1940; Tsetsevinskii, 1940; Chirkova, 1955; Kopein, 1959; N.N. Spitsyn), but, apparently, not in the extreme northern edge of the peninsula (Table 21), where the tundras exist on a very flat plain. Along the Venui-euo, Tiutei, Kharosovoi, Se-yaga, Morade and Tambei rivers, burrows of arctic foxes are particularly abundant. At places in the middle course of the Tiutei river, burrows are located at a distance of only some tens of meters from each other. The region of massive denning of arctic foxes in the maritime tundra of the southwestern coast of Baidaratsk Bay connects with the best arctic fox lands on the Bol'shezemel'sk tundra. Some authors consider that in 1/2 of the entire Yamal territory, burrows are few, and probably only in 1/4 of the territory are they met with frequently. It is suggested that in Yamal, there are about 10 thousand burrows of arctic foxes; this constitutes 1/3 compared to the Bol'shezemel'sk and Malozemel'sk tundras. Judging by the abundance and catches of arctic foxes, it is evident that the number of burrows here is considerably greater (see the first footnote to Table 21).

Already at the end of the last century, Nosilov (1909) who wandered in Yamal for more than 2 thousand km, could see only 6 arctic

Table 20. Combined table of the calculation of arctic fox populations

Region, author	Area	Time of calculation	Number of polar foxes
Kola Peninsula, Iokan'go-Ponoisk tundra	Entire territory		1000-2000
Kil'din Island; Formozov, 1929; Boitsov, 1937	Entire territory 7500 ha. On 1000 ha.	1927, August-September 1932, summer	Not more than 35-40 adult pairs; 534 ¹² to 5 pairs; 71 ¹²
Bol'shezemel'skaya and Malozemel'skaya tundras; Skroblov, 1958	Entire territory On 1000 ha.	1953-1955	15,500 ¹³ 0.8-2.2
Novaya Zemlya; Dubrovskii, 1937	Entire inhabited territory	1932-1933 1935-1936	~4,000 More than 8,000
Trukhansk territory: below 69-70° N. Lat.; Boitsov, 1937	On 1000 ha.	1926	1
Taimyr Peninsula, Nizhnyaya Taimyra river; Sdobnikov, 1958	On 1000 ha.	1947, September	3.8
Delta of Lena river, region of Tiksi; Freiberg, 1939	On 1000 ha.	1932, November-January	0.1-1.3
Magadan district; Shustov and Belozorov, 1959	On 1000 ha.	1956-1959	0.25-2.25
Commander Islands, Bering Island; Freiberg, 1926; Tikhenko, 1929	Entire territory of the island On 100 ha.	1924 1928	~2,000; ~3,500 ¹⁴ 1.3; 2.3
Mednyi Island, Freiberg, 1926; Tikhenko, 1929; Boitsov, 1937	Entire territory of the island On 100 ha.	1924; 1925; 1928 1924; 1928	~800; ~1000 2.0-5.0

¹²All ages.¹³From average yield.¹⁴Except migrants.

Table 21. Combined table of calculation of arctic fox burrows

Region, author	Year	Area	Number of burrows
Kanin Peninsula; Shibanov, 1951	1945-1947	On 1000 ha.	0.7-5.8 (from 1000 burrows)
Bol'shezemel'sk and Malozemel'sk tundras; Skrobov, 1958	1953-1955	Entire territory of the tundras On 1000 ha of various subzones	130,000 1.8-5.0 average of 3.2
Yamal Peninsula; N.N. Spitsyn; Tsetseviniskii, 1940	1927 1932-1934	Entire territory On 1000 ha.	10,000 ¹⁵ average of > 1-2
Gydansk Peninsula and Maliy Yamal		Entire territory of the tundras	9,000-10,000
Tundras of Turukhansk territory below 69-70° N. Lat; Boitsov, 1937	1926	Average over 50 km ² On 1000 ha.	1 (from 71) average of 0.2
Dikson Island	1940's	On 1000 ha.	1.8
Lower Yenisei river (Omulevaya, Varguzino, Gol'chikha); A.F. Chirkova	1940's	On 1000 ha.; in places on 1 km ²	2.9 7-8
Taimyr Peninsula, eastern coast of Khatangsk gulf north of Gusikhi river; A. Romanov, 1941	1940	In 100 km ² (from total area of 500 km ²)	average of 5.0 (from 25)
Lena-Khatanga territory; A. Romanov, 1941	1926-1927 and 1933-1934	Entire territory of the tundras On 1000 ha.	6,000 ¹⁶ 0.05-0.5
Commander Islands, Mednyi Island; Cherskii, 1919-1920	1918 and earlier	Territory of the coastal zone	Inhabited-75
Bering Island; Suvorov, 1927	1915-1916	In an area of 20 "ukhozhei"	Inhabited-204 Uninhabited-105

¹⁵According to Skrobov (1963), about 22,200 burrows.¹⁶Total number of periodically inhabited burrows.

foxes, but the Nenety [native people] told him that "arctic fox was found not a long time ago and it was encountered on each verst". In our time in northern Yamal, in the summer, in a year of average "yield" (1949), the number of arctic foxes met with during one day's journey by sled* is 1–2, and in winter up to 10 tracks were encountered; in the Pri-Ural region in August, up to 10 arctic foxes and in winter 2–5 animals. In the Mare-Sale region on the western coast of Yamal in autumn, they used to wander in tens, and only after the freezing period did their numbers sharply decline. On the coast of Baidaratsk bay, in the middle of August 1947, in a year of abundance, on a walk of 80–100 km, more than a hundred arctic foxes were counted and in winter, at places for 1 km, there were 1–2 arctic foxes and 3–5 tracks. Deep in the tundra, arctic foxes were significantly fewer; on a journey extending for 80–100 km, only 10 foxes were met with. With an abundance of animals in southern Yamal in the winter of 1947/48, the hunters caught from 15 to 35 arctic foxes for the season, and in the best conditions, up to 70. In a drive on an area of 20–30 km², 40–60 arctic foxes were taken in December–January 1955/56 and in February–March, 20–30. In the years when their numbers are depressed, on a week's excursion in the tundra, 2–3 tracks were encountered and only isolated arctic foxes were caught in the season; it was only the best hunters in southern Yamal who were able to take 10–15 individuals (A.F. Chirkova).

The total number of arctic foxes in the Yamal region after the end of the harvest season for 1955–1958 was 3.1–3.6 thousand head—1/4–1/5 of those, that were in the hunting period (12.4–17.6 thousand per year). The degree of harvesting was 70–80% of the population (Smirnov, 1959). However, judging by the number of arctic foxes hunted in this region, in which a considerable part of the territory was still insufficiently developed for harvest, one may presume that the number is considerably greater, especially at the beginning of winter.

In the northern part of Gydansk peninsula and in the Malyi Yamal peninsula, along the Poilovo and Le-Yakha rivers, a large concentration of arctic fox burrows is observed. In the territory of the latter 21 sections with abundant burrows were revealed by an aeroplane. The number of burrows in the Gydansk peninsula and Malyi Yamal is assumed to be equal to the number in Bol'shoi Yamal (Table 21). But, considering the extent of territory of the Gydansk

*Russian word is *narta*, which means both dog- or reindeer sled—Sci. Ed.

peninsula, the sparse settlement and poorly developed harvest of arctic foxes, a significantly greater number of burrows may be expected here.

In the north of Krasnoyarsk territory, arctic fox is comparatively densely settled in the tundra of the lower Yenisei, along Pyasina river and in part the northeastern Taimyr peninsula (Rutilevskii, 1939; Shastin, 1939; A. Romanov, 1941; Chirkova, 1955; Tables 20 and 21). In the Avamsk tundra, burrows in places are encountered at a distance of 10 km from each other. In northern Yakutiya, the western regions are richer in arctic foxes than the eastern ones. There are many arctic foxes on the New Siberian and Lyakhovsk islands and between the Lena and Indigirka [rivers] (Konstantinov, 1921; Tugarinov, Smirnov and Ivanov, 1934; Freiberg, 1939; A. Romanov, 1941).

- 212 In the Lena-Khatanga territory, the density of burrows declines from north to south. In summer, the maritime tundra between the Khatanga and Anabara, between Anabara and Olenek north of the Pronchishchev range, and between the Olenek and Lena in the region of the Chekanovsk range are densely inhabited. More than half of the total number of burrows in the Lena-Khatanga territory (6000 burrows) are located in the northern subzone of the tundra; the shrub tundra is the most poorly inhabited. There are many burrows in the Lena river delta. Now and then, burrows are met with at a distance of 200–250 m to 0.5–1 km from each other, but are usually scattered tens of kilometers from each other (A. Romanov, 1941). In unfavorable years, the number of arctic foxes here in winter is not large. In Anabarsk and Ust'-Yansk regions, an accumulation of burrows is noticed only in some places. In the upper Baranikhi river, near Kolyma, F. Vrangeli' (1841) found numerous burrows of arctic foxes in the past century.

In the years of low numerical level in the Lena delta, the baited traps with an effective radius of about 300 km² took in from 4–6 to 30–40 arctic foxes in the winter of 1932 (Freiberg, 1939); the probable population density—up to 1.3 polar foxes per 1000 ha. When the total number of arctic foxes was high in northern Yakutiya in the lower Indigirka and Kolyma in the winter of 1946/47, the average hunter in one day's harvest encountered up to 13 arctic foxes; the ordinary hunter caught about 50, and the best one caught 183, for the season. With low numbers in the 1948/49 season on a journey of 20–50 km, both in the northwestern and northeastern regions of Yakutiya,

hunters rarely met with more than 1–4 arctic foxes; of them the average caught 10 for the winter, and the best 20–30 animals. Arctic foxes are quite numerous on Wrangel' Island (Mineev, 1935; Sergeev, 1936).

In extreme northeastern Siberia (Magadan district), the average density of fox populations in tundra subzones differ by a factor of 10-fold (Table 20) (Shustov and Belozorov, 1959). In Bilibinsk region of this district in the winter of 1948/1949, in a year of quite large numbers of animals, the best hunters took up to 40 animals (Chirkova, 1955). The arctic fox was scarce in the 30's on the Bering Sea coast from Korf Gulf to the mouth of the Apuka river (Koryaksk Nats. Region), it was hunted singly and rarely in tens in each region (Samorodov, 1939).

Estimates of arctic foxes on the Commander islands are known from the first decades of the present century (Tables 20 and 21). On Bering Island, the total number of arctic foxes changed through the years from approximately 2 to 4 thousand, and on Mednyi Island was in the range of one thousand; the population density on the latter island was 2 or more times greater. The considerably great density of the arctic fox population on the Commander islands, as compared to the mainland, depended at the end of the past century and the beginning of the current one, on the abundance of marine animal carcasses and from the 20's—on the systematic provisioning of the arctic foxes.

For the historical period in the USSR*, the number of arctic foxes changed to the reduced side, chiefly on isolated islands where there were numerous blue foxes (Krasheninnikov, 1755; Steller, 1774, 1781; Gondatti, 1898; Nosilov, 1909; Formozov, 1929). Mention by Krasheninnikov concerning the large quantity of arctic foxes on Kamchatka, and Steller's description (1774) of the innumerable herds of these animals in the middle of the 18th century, are known; the latter killed in one day up to 70 arctic foxes with an axe. The large number of arctic foxes on the shores of the Bering Sea in the past century and earlier, when arctic foxes in "hundreds ran along the shore" depended upon the abundance of marine animals, on the carcasses of which, the arctic foxes were feeding.

There were large numbers of arctic foxes on Novaya Zemlya at the end of the 80's and on Kil'din Island in the 70's of the past century with the first permanent appearance of humans. One needs to assume that the number of arctic foxes on the Kola peninsula and in

*From the citation dates, this apparently refers instead to Russia—Sci. Ed.

the northern Far East, also greatly decreased, where the best coastal places for polar fox settlement are now densely inhabited by man. There are some data about significant decreases in stocks of arctic foxes in Sweden (Lost, 1955).

- 213 *Habitat.* Arctic foxes prefer open tundra areas where it also reproduces. Only in the years of high numbers and insufficient unoccupied habitations do arctic foxes breed among shrubby vegetation. The southern border of the denning area coincides with the northern limits of distribution of tundra-edge forests. Southward, burrows of arctic fox are only found in broad expanses of montane tundra. In connection with the climatic warming in the Arctic in the course of the last series of decades, a shifting of arctic foxes from the southern belt of tundra to more northerly subzones is observed (Skrobov, 1960, 1960a).

The main factors which regulate the distribution of the species in the period of sedentary life are the relief of the locality and the food conditions. The most suitable places for denning are hilly landscapes of dry open watersheds and sources of rivulets and streams; small



Fig. 83. Tundra along the Khatanga at 72° N. Lat., Taimyr. Core fox habitat in summer. Photograph by A.F. Chirkova.

sandy knolls in open tundra; the upper parts of high terrace slopes of creek valleys, the borders of terraces above floodplains, elevated lake shores, islands and seashores. Near the southern boundary of the range in the summer time, arctic foxes den in treeless rocky slopes of mountains, mainly northern exposures, and also in high open watersheds. Burrows here are always situated on elevated sections of tundra.

Places of denning and feeding usually do not coincide. Denning regions change annually. In years with an abundant "yield" of lemmings, a large number of arctic foxes live in the arctic and subarctic tundras. With a depression in rodent numbers, arctic foxes remain on the seashore, in the southern subzone of tundra and forest-tundra; in optimal years, the arctic fox usually does not live in the latter.

214 Near the seashore, in connection with better security of food, the arctic fox population is more permanent than in other zones. As is known, habitats are abruptly changed seasonally throughout the year in connection with migrations. Places where small rodents are found in superabundance serve as feeding biotopes; at any time of year in summer, moreover, such places are those where waterfowl occur. In winter, arctic foxes also feed along the shores and in areas where willow ptarmigan [*Lagopus lagopus*] are concentrated.

In the Kola peninsula, breeding places of the arctic fox are restricted to hilly landscapes at a distance of 40–50 km from the sea. The arctic fox constructs the burrow in bearberry-reindeer moss, hilly, lacustrine tundra and on alluvial meadows, and forages chiefly in willow-grass, sedge, lacustrine, and rocky stand-types, and along the seashore. On Kil'din island, it often lives in coastal biotopes (Formozov, 1927; Dubrovskii, 1939; Zolotov, 1940). On Novaya Zemlya, arctic foxes densely inhabit the low-lying Gusinaya Zemlya with its hilly landscape in the southwestern parts of the island; fewer arctic foxes occur in montane tundra at Matochkin Shar; in the polar part of Severnyi Island which is covered with an ice shield, arctic foxes are found only along the sea coast (Zhitkov and Buturlin, 1901; Nosilov, 1909).

The dispersion of burrows in Kaninsk, Timansk and Malozemel'sk tundras is closely connected with sandy-hilly tundra (Shibanov, 1951; Maksimov, 1959). In Malozemel'sk and Bol'shezemel'sk tundras, 93% of the burrows are located on hillocks, knolls, slopes of ravines and along the shores of water bodies. Of the burrows 75.5% were placed among types of tundra vegetation, of which 22.5% were in moss, 18% in lichen, and 16.1% in shrub formations. 13.8% of the

burrows were located within marshy tundra, of which the most frequent type—9.3%—were found in the vicinity of marshes in grassy-tundra, 10.5% were found in shrub tundra, and in meadow associations, 0.2% of the burrows (Skrobov, 1958).

On the Taimyr peninsula, the number of burrows dies away towards the north, as a function of the transition from the tundra zone to the arctic desert zone. On the Chelyuskin peninsula, burrows are absent. Burrows are rarely found along the coast of the Kara Sea, are relatively frequent along the northern shore of the peninsula and along the Nizhnaya Taimyr river. Along the entire western shore of the peninsula, the coastal and pre-delta sections, and river and creek banks are the areas most densely inhabited by arctic foxes. On the eastern coast and on Begicheva Island, their burrows are often situated in hilly tundra. In the north of the peninsula, the arctic fox reproduces among cotton grass-sedge-moss tundra, where there is a rich fauna of rodents and birds, and also along the edge of stony deserts, along ravines and in glacial cirques on the montane plateau of Byrrang. Burrows are dispersed among dryas patches and grass-moss in the arctic semidesert (Koshkin, 1937; L. Lopov, 1939; Shastin, 1939; Sdobnikov, 1959).

In the Lena-Khatanga territory, satisfaction of the basic nutrition of the arctic foxes is associated with tundra intersected by a dense network of small creeks, lakes and *laidas**, lake depressions, and the seashore, which are the main feeding lands of arctic fox (A. Romanov, 1941). On Wrangel' island, the arctic fox lives among sandy hillocks and feeds along the seashore.

In the basin of the Anadyr' river, the arctic fox thrives abundantly in the continental and maritime arctic level tundra, but are also abundant in the hilly shrub tundra. There are small numbers of arctic fox in montane lichen-shrub tundra and in the forest tundra, and a negligible number in the level shrub tundra. In alpine tundra the animal is absent. In the montane tundra region of the southeastern part of the Koryaksk National Region, the small number of arctic fox here are restricted to tundra, the seashore and among shrubs in river valleys (Mineev, 1935; Mikhel', 1937; Gassovskii, 1939; Samorodov, 1939).

In Magadan district, the density of foxes is highest in the northern maritime subzone; in the southern maritime subzone, its density

*Openings in the forest-tundra landscape—Gen. Ed.

is less, and in montane sections of the central interior subzone which are far from the sea, its density is lowest. In 1000 ha of different types of hunting lands the distribution of arctic foxes is, on the average, as follows. In flooded shrubby and meadow tundra—biotopes
 215 favorable for reproduction—5 arctic foxes. In complex marshes, in the lower courses of large rivers, and along level watersheds and maritime plains with abundant lakes—the main biotopes of arctic fox in the period of reproduction and raising of young—2.25 arctic foxes. In the low-lying and transitional marshes and marginal shrub tundras—1.3 arctic foxes. In hummocky, cotton grass-sedge, and oiser shrub tundra of the northern subzone—0.75 arctic foxes. In tundra, shrubland and marshes of the southern and central subzones of the arctic tundra—0.5–0.25 arctic foxes (Shustov and Belozorov, 1959).

In Kamchatka, the arctic fox inhabits the zone of sparse stone-birch forests. On the Commander islands, it dens in maritime hillocks and rocks and, in fewer numbers, lives in the interior of the islands. It feeds, mainly, in the *laidas*, cliffs of bird colonies, and along the banks of rivers; in autumn, in tundra and on hills. Throughout the year, they frequent human settlements (Suvorov, 1912; Barabash-Nikiforov, 1937).

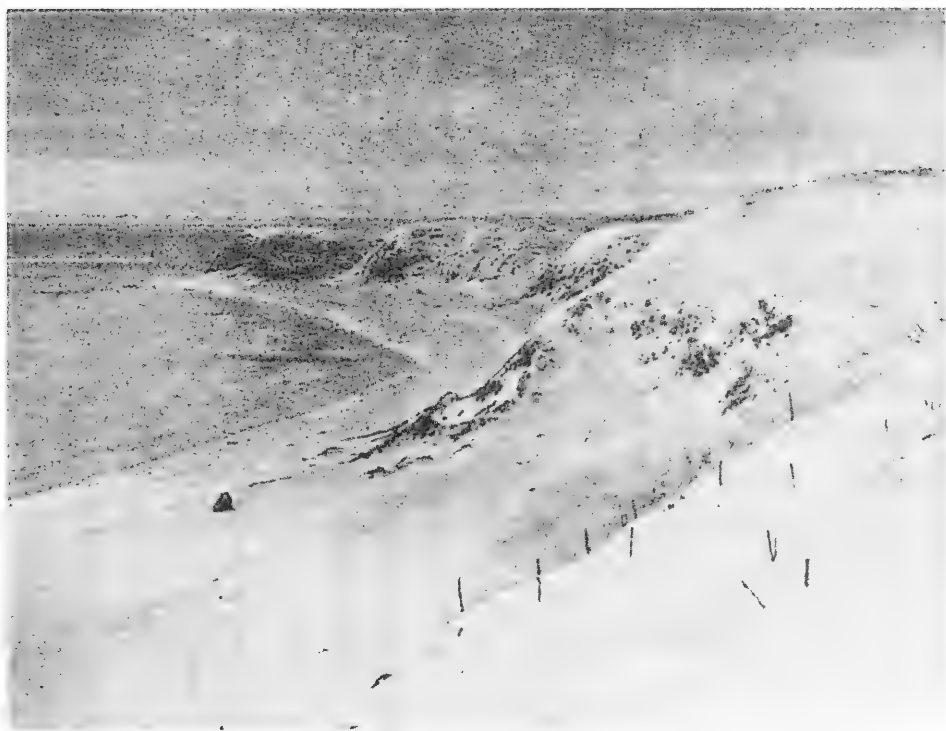
In winter, the arctic fox is often encountered on ice. During the time of migration to the forest zone, they stick to open places—river valleys, watersheds, fields and marshes.

Food. The arctic fox, like the red fox, is an omnivorous beast, but more voracious and less selective; it is poorly provided with food and is frequently hungry for long periods. Within the USSR, more than 125 species of animals and 25 plant species are known to be eaten by the arctic fox.

The nutrition of the arctic fox in continental tundra and on the seashore differs sharply. Already investigators of the past century had emphasized the dependence of arctic fox on lemmings (Pakhtusov, 1842; Krivoschapkin, 1865; Middendorf, 1869; Tret'yakov, 1871;
 216 Silant'ev, 1898). At the present time, numerous investigations have shown that the main food of tundra arctic foxes are small rodents, which constitute in some seasons and years more than 99.0% of the stomach contents and feces; mainly the species represented are Norway, Ob and hoofed [= collared] lemmings (*Lemmus lemmus*, *L. sibiricus*, *Dicrostonyx torquatus*). Gray (genus *Microtus*) and red [backed] (genus *Clethrionomys*) voles are eaten by arctic fox in smaller amounts; these rodents are met with in the arctic fox's diet mainly in

the southern tundra belt, in forest tundra and in the taiga zone (during migration). In places of water vole (*Arvicola terrestris*) abundance, arctic fox feeds also on them; they rarely catch arctic hares which are particularly characteristic of the shrubby growths on the Bol'shezemel'sk tundra (up to 43% in studies).

Birds are caught more often in spring and summer (in Yamal up to 52% occurrence in analysis). They destroy nests, eating the eggs and nestlings; in the second half of summer, they hunt molting geese, most frequently the white-fronted goose, and rarely, ducks. In autumn and winter, they catch willow and rock ptarmigan [*L. lagopus*, *L. mutus*], rarely snow buntings [*Plectrophenax nivalis*] and longspurs [*Calcarius lapponicus*], and still more rarely, birds of prey wintering in the tundra. Quite often they eat fish (up to 41% occurrence in the food analysis), usually refuse of fish harvest or bait; it sometimes catches migrating salmon during spawning time,



Wild and domestic reindeer are of great importance in the nutrition of tundra arctic foxes, herds of which arctic foxes usually follow. In the diggings [feeding craters] of reindeers, the arctic fox catches small rodents; near the reindeer herd, ptarmigan are concentrated; fallen reindeer become food for arctic fox (up to 68% in food remains in famine years). In winter, arctic foxes eat the feces of reindeer. Sometimes, arctic foxes pursue reindeer weakened by a prolonged period of ice-covered ground or injured reindeer; they devour lumps of snow moistened with the blood of these animals; they lie around the dying animals in expectation of their death. Cases are known when arctic foxes killed and ate new-born reindeer fawns, even in the presence of their mothers.

Most of the above-listed foods are eaten by the tundra arctic fox only in the absence of lemmings. One must consider them secondary.

Invertebrates, especially marine, are insufficiently known. Insects occur rarely and in negligible quantities in the food of the arctic fox—beetles, bumblebees, wasps, grasshoppers. Extremely rarely, the arctic fox eats amphibians (grass frog on the Kanin peninsula). Weasel, ermine, shrews, insects and amphibians must be assigned to the class of accidental and emergency food, eaten in the years of lemming scarcity.

Cannibalism is developed to a strong degree among arctic foxes. In some years, more than 50% of those animals falling into traps, were found to be chewed. Cases of eating dogs and red foxes are extremely rare¹⁷.

Arctic foxes inhabiting islands and coasts feed on the flotsam of the sea—carcasses of marine animals and birds. They gnaw a way through the whole system of a whale's carcass and sometime do not come out of it for some days (Nosilov, 1909; Mineev, 1935): they gorge themselves with blubber until they vomit. On the littoral, they gather cast-up cod, haddock, sea-hen, capelin, arctic cod, *navaga* [*Eleginus navaga*], smelt and other fishes. There, they also gorge on echinoderms, crustaceans, molluscs, sea-cucumbers, ascidians, sponges, hydroids and others. In a period of massive consumption of sea urchins, the teeth of arctic foxes on Mednyi Island are stained violet in color. Bird colonies are preferred foraging places for arctic fox. They capture black guillemots [*Cepphus grylle*], murres [*Uria* sp.], fulmars [*Fulmarus glacialis*], razorbills [*Alca torda*], gulls and even the stronger skuas [*Stercorarius*], cormorants, goosanders [*Mergus*] and

¹⁷0.4–2.0% in analyses of food (Pereleshin, 1943; Skrobov, 1958).

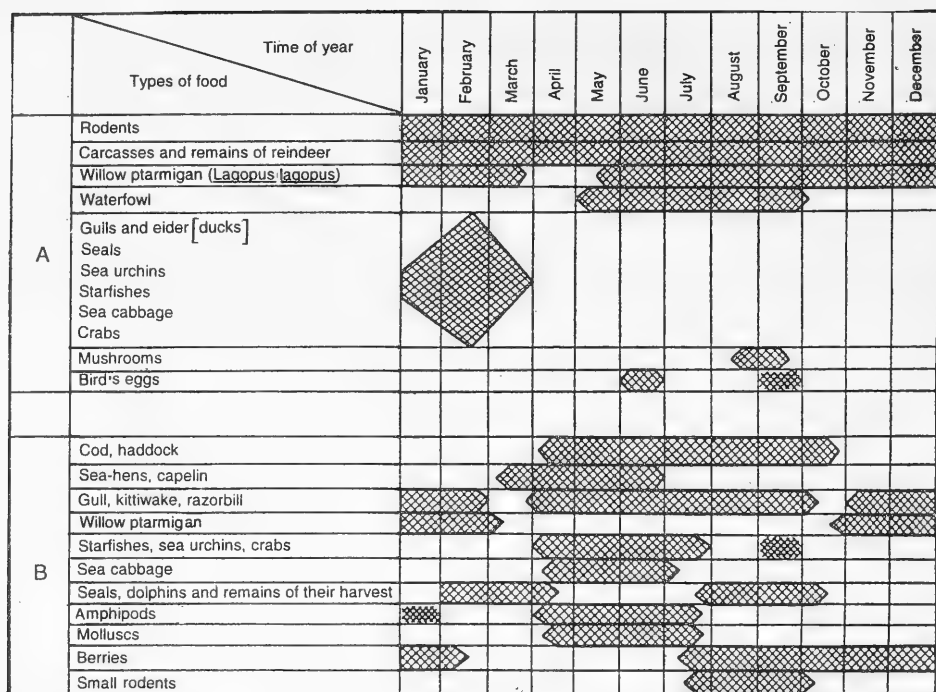
others. In one feeding, a hungry arctic fox may eat up to 0.5 kg meat, fat and fish (Skrobov, 1958). The gastro-intestinal tract of the arctic fox fully rids itself of food remains within 24 hours (Pozgnyakov, 1957).

217 Arctic foxes feed also on plant food; in the tundra on various fruits—crowberry, blueberry, whortleberry, bearberry, cloudberry, various species of sedges and grasses, and on the seashore, on seaweeds; the significance of the latter is not entirely clear, since it is evident that they are not digested at all. Arctic foxes chew on russula mushrooms. In the alimentary tracts of 898 arctic foxes were found 78 different species and forms of plants taken during feeding on other food materials (Pereleshin, 1943). For the arctic fox, as for the red fox, ingesting inedible material—discarded reindeer skin, raw strips, rags, string, paper, woodchips, crushed pieces of coal, pieces of soap, as well as pebbles, sand, glass fragments and others—is characteristic.

On moving in autumn and winter to the ice of the Arctic Ocean, arctic foxes (especially the old ones, for which independent foraging is difficult) usually follow polar bears, gathering its food leavings, and also remains of the food of ringed seals; they gnaw at the erucations of the walrus—a whole pile of indigestible food. Arctic foxes return in spring from the ice seriously emaciated.

The prevalence in the diet of these or other food items depends upon the season of the year. Tundra arctic foxes most frequently consume lemmings at the end of summer, in autumn and in the first half of winter, i.e. at the time of their mass appearance. The most stressful time of the year in tundra is the end of the winter and beginning of spring. The long duration of ice-cover, often in the second half of winter, results in the emaciation and death of reindeer, thus providing additional food for arctic foxes; at that time, the ice crust which forms renders difficult the excavations of voles and causes the death of small rodents. At that time, arctic foxes with broken claws are not infrequently encountered. In spring and summertime, the possibility of the foxes' feeding at the expense of birds increases. In the second half of summer, the molting birds appear, and in autumn berries ripen.

218 The diet of the arctic fox varies in different geographic regions. In Iokan'go-Ponoisk tundra of the Kola Peninsula (Table 22), at the time of rodent reproduction, the arctic fox most frequently feeds on Norway lemming (to 96% of all data), they often eat gray and red-



217 Fig. 85. Change in the composition of arctic fox diet during the course of the year. A—mainland arctic fox of Kola peninsula (Zolotov, 1940); B— island arctic fox of Kil'din Island, Murman (Formozov, 1929; Zolotov, 1940).

backed voles, birds and insects. On Kil'din Island in the summer of 1927, foxes mainly existed at the expense of the shore fauna due to the scarcity of rodents (Fig. 85; Formozov, 1929).

In the northern parts of the Kanin Peninsula (Tables 23 and 24), feces collected near the den burrows of arctic foxes contained, almost exclusively, mammalian remains. The majority of them belonged to collared and Siberian lemmings, and in lesser quantity, voles and others. In a year when lemmings were absent, cloudberry was predominant among plant foods. In Bol'shezemel'sk and Malozemel'sk tundras (Table 23), the diet of the arctic fox consisted most frequently of mouse-like rodents, including Siberian lemming, and when the latter was in small numbers, narrow-skulled vole (*Microtus gregalis*) and water vole (at the mouth of the Pechora); moreover, white hare and, among birds, chiefly willow ptarmigan (probably the latter, as well as hares, represented bait from traps*). Remains of shrews

*The Russian phrase, "nazhivky iz samolovov", probably refers to bait from a dead-fall trap; see Figs. 96, 97—Sci. Ed.

(winter, 1957/58, up to 8% occurrences) were found in arctic foxes caught near Karsk Bay. Fox stomachs in the winter of 1956/57, when lemmings were absent, contained much garbage and household refuse. Around burrows of the arctic fox in summer are often found wings and bones of willow ptarmigan, and rarely, of ducks, small shore-birds and small passerine birds and among mammals, the white hare (Skrobov, 1958).

The nutritional condition of arctic foxes in northeastern Bol'shezemel'sk tundra depended on the nutritional conditions of the year, as well as on sex, age, and physiological condition. In winter 1956/57, distinguished by low numbers of small rodents and large numbers of arctic foxes, males were in better condition in autumn, while during winter they lost weight. Females, especially those with

Table 22. Diet of arctic fox on Kola Peninsula (in % of occurrences in number of investigated objects)

Food	Place of collection, season, year	Iokan'go-Ponoisk tundra			Kil'din Island, 1927, Summer ²⁰
		1935			
		Summer ¹⁸	Winter ¹⁸	August ¹⁹	
Small rodents				80	20
Lemmings		96	92		
Gray voles [<i>Microtus</i>]		46	15		
Common and Northern red-backed vole [<i>Clethrionomys</i>]		42	13		
Arctic hares [<i>Lepus timidus</i>]			1.3		
Shrews [<i>Sorex</i>]			1.3		
Carrion (reindeer)			9	18	
Birds		42	29	16	40
Fish				10	
Insects		29			Less than 5
Marine animals of the littoral zone					25 ²²
Crustaceans				2	
Molluscs				2	
Plants		17 ²¹		4	Less than 5
Refuse			11		
Number of small rodents				Very low	Low

¹⁸L.N. Borodin.

¹⁹Zolotov, 1940.

²⁰Formozov, 1929.

²¹Berries.

²²Mostly sea urchins.

Table 23. Arctic fox diet in tundra of northern Arkhangel'sk district (in % of the total number of occurrences in investigated objects and in % of total weight of remains)

Food	Place of collection, amount of objects, season, year		Northwestern Kanin Peninsula ²³		Bol'shezemel'sk and Malozemel'sk tundra ²⁴		Karsk Bay ²⁵	
			554	604 excrements	155 stomachs	50 stomachs and intestines		
			% of findings		% of weight		% of findings	
			Summer		Winter		Winter	
			1946	1947	1955/56	1957/58	1956/57	
Mammals			83.3	72.4				
Small rodents					11.0	72.4		24.7
White hare					43.3	5.3		7.4
Shrews				negligible				1.0
Carrion (reindeer)					7.3	2.7		4.6
Marine animals					0.6	12.8		2.8
Birds			6.4	11.2	7.0 ²⁶	3.8 ²⁶		5.6
Bird's eggs						3.0		
Fish			0.1		29.2	0.1		6.5
Insects			4.5	11.3				
Crustaceans			0.3					

Molluscs	0.1	0.4			
Arctic fox	negligible	negligible	0.3		14.8
Plants	5.2	4.7			
Inedible objects (rags, leather, nets, mineral compounds and others)			1.6	0.1	25.7
Household refuse	0.1				6.5
Total in %	100	100	100	100	100
Number of small rodents	<div>in 1946, medium</div> <div>in 1947, sharp decrease in number</div>				
			Low	Medium	Low

²³Shibanov, 1958

²⁴Skrobov, 1958.

²⁵Chirkova et al., 1959.

²⁶Mostly remains of willow ptarmigan.

219 litters, were more emaciated in autumn, but in winter, they fattened up; only a few specimens were characterized by severe emaciation—purplish color of muscles and great projection of bones. At the same time, arctic foxes which were, apparently, feeding on the coast, were noted to have large fat deposits—subcutaneous fat on the sides up to 2–3 cm, and in the form of layers in the muscles. From one male, up to 1 kg of fat was removed, which represented 1/4 of its carcass weight. In the following winter 1957/58, distinguished by abundance of lemmings and low number of arctic foxes, the young females were very well nourished, but those which reproduced became of lower than average nutritive condition (Chirkova et al., 1959).

Foods of the arctic fox on the islands of Novaya Zemlya are varied. The animals move back and forth everyday from the tundra in which they catch lemmings, to the coast where they feed on marine flotsam. In rivers, they catch chars and live around the carcasses of marine animals for long periods in snow burrows. Hunting in bird colonies, they destroy completely the accessible nests. In Franz Josef Land, the arctic fox feeds mainly at the expense of bird colonies (Nosilov, 1909; Esipov, 1935).

220 Yamal arctic foxes, far from the coast (Table 25), fed exclusively on terrestrial mammals (in 1939–1942 up to 99%–100% of occurrences in diet; Dunaeva and Osmolovskaya, 1948), and sometimes uninterruptedly on mouse-like rodents. In summer 1933, in the Tambei river basin, the latter formed 99.6% of occurrences in feces at the burrows (Tsetsevinskii, 1940). They were mainly Siberian lemming (up to 79.5% of occurrences from total sample amount and up to 92.5% of all rodents in northern Yamal), and fewer collared lemmings, and also gray and red-backed voles. The importance of lemmings, especially the Siberian, increases as one moves northward on the peninsula. At places in the floodplain of the Ob' river and Ob' Bay, water voles occupy some place in the diet of the arctic fox. The portion of birds in the diet of tundra foxes with lemmings abundant is not great even in summer, but in individual years in the taiga belt of the Yamala-Nenetsk National Region, it increases greatly (to 50%). Here, the arctic fox gorges on fish, mainly the sorts of refuse from places of fishing harvest. In a year of abundant berry crop and few lemmings, plant food is of great importance and also carrion.

Great fluctuations in the dietary composition is observed in the tundra arctic fox, depending on annual abundance of lemmings (for example, winter 1932/33 and 1933/34—Table 25: Tsetsevinskii, 1940).

In winter 1938/39, in southern Yamal (Korzinkina, 1946), the occurrence of rodent remains in the arctic fox diet was observed to grow monthly in connection with subnival lemming reproduction. Bird remains also declined. With an abundance of rodents in autumn 1939 and their gradual disappearance in winter 1939/40, the occurrence of rodent remains in the stomach contents diminished monthly; at the same time, the arctic fox fed more often on reindeer carrion and caught birds.

On the Taimyr peninsula, the principal food of the arctic fox also consists of small rodents. In August 1931 on the right bank of the lower Khatanga river, among the bones of mouse-like rodents collected near an old den burrow, 85% of the skull remains consisted of 222 collared lemming, and 15%—Siberian (A.F. Chirkova). In winter 1932/33 in the neighborhood of Khatanga village and a series of eastern stations* (Table 26; Skalon, 1936) with a lemming die-off, small rodents occurred in 68% of the dissected stomachs of arctic foxes; predominantly voles—*M. middendorffi* and *M. hyperboreus* and the Siberian lemming. The remains of reindeer carrion, fish mainly from baits, and also willow ptarmigan and some other birds constituted the three other types of food; each of them was found in nearly 1/3 of the stomachs. The considerable mixture of food and inedible human household refuse was also an indication of the lack of small rodents in that winter.

On the southwestern coast of Taimyr and on Begichev island, the principal food of the arctic fox was also recognized as lemmings, especially the Siberian. On the Chelyuskin peninsula, in a lemming 223 year, the remains of collared lemmings—the only one occurring here—constituted the principal content of tundra arctic fox feces. In years when rodents disappear, the diet of the arctic fox mainly consisted of marine flotsam which is not present here each year owing to the different times of ice formation, and of the leavings of the polar bear. Arctic foxes fed in autumn 1932 on marine flotsam. The foxes also dug this food out from under the snow in winter, living in a series of snow burrows. In winter time, arctic foxes here frequently do not get enough to eat, and in connection with this cannibalism develops among them. In the famine winter of 1944/45, arctic foxes dug up the lemming carcasses stored from the preceding year, when these rodents

*In the original Russian text, this word is *stankoy* (gen. pl.; machine-tool); apparently a misprint for *stantsov*—Sci. Ed.

220 **Table 24. Mammalian species in food remains of the arctic fox on Kanin Peninsula in summer at burrows (in % of total number of occurrences in feces; Shibarov, 1951)**

Food	Quantity	554	604
	Year	1946	1947
Collared lemming [<i>Dicrostonyx torquatus</i>]		56.8	48.9
Siberian lemming [<i>Lemmus sibiricus</i>]		21.1	8.4
Wood lemming [<i>Myopus schisticeps</i>]		0.5	0.2
Lemmings, not accurately identified		0.4	—
Root vole [<i>Microtus oeconomus</i>]		3.3	4.0
Northern red-backed vole [<i>Clethrionomys rutilus</i>]		—	0.3
Voles, not accurately identified		10.4	30.4
Mouse-like rodents, not accurately determined		5.7	6.6
Shrews [<i>Sorex</i>]		—	0.2
Arctic fox		1.8	1.0
		100.0	100.0

were abundant, and died after that (Kirpichnikov, 1937; Koshkin, 1937; Rutilevskii, 1939; Sdobnikov, 1958).

In Lena-Khatanga territory (Table 26) during a sharp reduction in numbers of mouse-like rodents, mainly collared and Siberian lemmings were found in the stomachs of half the arctic foxes in winter 1926/27. The foxes took birds and fish more often from lures (A. Romanov, 1941). In the lower Lena, the arctic fox also preys on northern pika—*Ochotona hyperborea* (Kapitonov, 1961).

In the eastern regions of northern Yakutiya (Table 26), the years in which the investigation of arctic fox diet fell apparently coincided with few rodents (Krasovskii, 1939). In the delta of Lena, the arctic fox frequently fed on fish and birds.

224 The existence of arctic foxes on the Commander islands is associated completely with the seashore. Their diet is composed (Table 27) of the carcasses of marine mammals, especially fur seals [*Callorhinus ursinus*] (up to 56% in the analysis), birds, echinoderms, mostly sea urchins, and other littoral invertebrates, fresh fish, and dried salmon from foodstores, crustaceans, and molluscs. Sometimes, arctic foxes capture young fur seals from their mothers, or drive away ringed seals from their breathing holes into the ice and then attack them. Cannibalism is not observed on the Commander islands. Among plant food, the arctic fox eats berries in the tundra, laminaria kelp,

Table 25. Arctic fox diet on Yamal Peninsula and Belyi Island (in % occurrences to number of investigated objects)

Food	Place of collection, number of objects, season, year	Yamal		Middle Yamal, in % of feces of mammals. Summer 1942 ³⁰
		Yamal		
		Arctic tundra, Tambai river. Winter ²⁸	From taiga to tundra ²⁹ , 898 stomachs and intestines in years (from-to) 380 stomachs. Winters of 1936/37-1938/39	
	Beyli Island, 53 stomachs Winter 1935/36 ²⁷	98 stomachs and feces. Winter 1932/33	163 stomachs and feces. Winter 1933/34	
Small rodents		94.9	51.5	79-97
Lemmings				95.4
Siberian lemming [<i>Lemmus sibiricus</i>]	49.1	92.5 ³⁴	75.0 ³⁴	86.8
Collared lemming [<i>Dicrostonyx torquatus</i>]		4.3 ³⁴	16.6 ³⁴	53.0
26				-
Gray vole [<i>Microtus</i> sp.]	33.8	4.3 ³⁴	3.6 ³⁴	8.6
Red-backed vole [<i>Clethrionomys</i> sp.]				
Water vole [<i>Arvicola terrestris</i>]				
Voles, not identified				0.6-0
Small rodents, not identified				
White hare [<i>Lepus timidus</i>]				4-18
Weasel [<i>Mustela nivalis</i>]				
Shrews [<i>Sorex</i>]				0.3
Carion of reindeer				
Marine animals	see below, supplemental food* ³²	15.3	1.2 68.1 0.6	up to 4 1-4 18-35
				0.3

(contd.)

(Table 25 contd.)

Birds (only feathers)	3.8	(3.1)	(11.6)	3-52 (4-22)	8.4-36 ³¹	3.6
Fish	3.8		1.2	0.2-22	0.5-3	0.3
Molluscs			1.2			
Supplemental food, lures, baits	67.9	bird feathers		Eggs and others		
Arctic fox	26.4	4.1 ³³	5.5 ³³	0.7-10		
Plants	3.8	77.8		71-95	3-21	
Inedible (rags, leather, nets, minerals, etc.)			24.4	2-10	0-5	
Household refuse	1.9			21		
Number of small rodents	low	lemmings		changing		very great
		great	negligible			

²⁷Tyulin, 1938.²⁸Tsetsevinskii, 1940.²⁹Pereleshin, 1943.³⁰Dunaeva and Osmolovskaya, 1948.³¹Mostly, willow ptarmigan.³²Ringed seal [*Phoca hispida*] and other marine animal fat.³³Moreover, arctic fox wool in 1932/33—20% and in 1933/34—71%.³⁴Of rodents.

*The Russian word "podkormka" apparently refers to supplemental food scattered on the ground to encourage local concentration of foxes—Sci. Ed.

222 Table 26. Arctic fox diet on Taimyr Peninsula and northern Yakutiya (in % occurrence to number of investigated objects to total of all occurrences)

Food	Place of collection, number of objects, season, year	Northeastern Yakutiya				
		Taimyr peninsula, found in stomachs. Winter 1932/33 ³⁵	Lena-Khatanga territory, total of all occurrences, 160 stomachs. Winter 1926/27 ³⁶	Lena delta, 1399 stomachs	Lyakhovsk islands, 207 stomachs. 1937-39	Middle Kolymsk region, 285 stomachs. Winter 1943/44
		1	2	3	4	5
Small rodents			68			6
Lemmings			32			
Siberian lemming [<i>Lemmus sibiricus</i>]			19.2	21.9	30.3	37.9
Collared lemming [<i>Dicrostonyx torquatus</i>]			2.6	33.1		
Gray voles [<i>Microtus</i>]			20.5	0.6		
Red-backed voles [<i>Clethrionomys</i>]			1.3	0.6		
White hares [<i>Lepus timidus</i>]			4			
Shrews [<i>Sorex</i>]			34.6	16.3		
Carion of reindeer					7.7	
Marine animals					0.5	3.1
Birds			28.2 ³⁸	3.1 ³⁹		2.1 ⁴¹
Bird's eggs			4		1.7	1.4
Fish			33.3 ³⁹	5.6	0.5	4.2
Arthropods					3.1	0.7
Supplemental foods, lures, baits		Fish and others	11.5	Mostly reindeer; fish; birds	4.9	
Arctic fox				2.5		

(contd.)

(Table 26 contd.)

1	2	3	4	5	6
Plants					
Household refuse	20.5 ⁴⁰	9.4	6.3	4.9	4.2
Empty stomachs		7.5	0.5	8.7	4.0
			6.1	46.8	42.4
Total %		100	100	100	100
Number of small rodents	Starting from autumn, large; in winter, small	Sharp decrease in the number			

³⁵Skalon, 1936.³⁶A. Romanov, 1941.³⁷Cha, 1953.³⁸Mostly willow ptarmigan.³⁹Mostly bait.⁴⁰Fresh plants.⁴¹Fat of marine animals.

223 Table 27. Arctic fox diet on Commander islands (in % occurrence to number of investigated objects to total of all occurrences)

Place of collection, number of objects, season, year Food	Bering Island		Mednyi Island	
	194 stomachs, to the total of all occurrences ⁴²	534 stomachs, to number of investigated objects, 1929/30 ⁴³	250 stomachs, to total of all occurrences, 1924/25 ⁴⁴	296 stomachs, to number of investigated objects, 1930/32 ⁴⁵
Small rodents	1.1	0.4		
Marine animals		0.2	56	6.8
Birds	2.1	2.2	4	39.5
Fish	38.4	10.3		14.9
		63.5 ⁴⁷		
Littoral marine organisms	32.4	15.7	20 ⁴⁹	30.1 ⁴⁹
				16.2
Crustaceans		3.4		others 25.0 ⁵⁰
Molluscs	2.5 ⁴⁶	1.1	1	23.0
Supplemental foods, lures, baits, household refuse	2.7		8	13.5
Plants	10.3	8.0	2 ⁴⁸	14.5
		19.1 ⁴⁸		
Inedible (rags, leather, nets, minerals, etc.)		0.6		
Empty stomachs	10.5	5.0	8	
Total in %	100		100	

⁴²Cherskii, 1919–1920.

⁴³Lavrov, 1932.

⁴⁴Freiberg, 1929.

⁴⁵Barabash-Nikiforov, 1937, 1939 (diet of tundra and not bait-fed arctic fox).

⁴⁶Octopus, dvuustika*

⁴⁷Dried fish—salmon

⁴⁸Sea cabbage.

⁴⁹Mostly sea urchins.

⁵⁰Insects—0.7%.

*Lit., trematode fluke; meaning unclear in this context—Sci. Ed.

rockweeds [*Fucus*] and other seaweeds of the littoral (Cherskii, 1919–1920; Freiberg, 1926; Lavrov, 1932; Barabash-Nikiforov, 1937a, 1939).

There are age and sexual variations in the nutrition of arctic foxes. Juveniles more often feed on lemmings. Among the Khatanga arctic foxes (Skalon, 1936), the lemmings are more often eaten by females than by males. Males caught mainly gray voles and also fed more on reindeer carrion or on baits of birds and fish and as a whole they did not show selectiveness in food. East of the Lena (Krasovskii, 1939), lemmings were also mostly found in the food of females. On Belyi island, differences in the diets of males and females were not observed.

Home range. A definite home range is characteristic of the arctic fox only in spring and summer, during the time of reproduction and growth of the young. On the Commander islands, at the time of den establishment and then the emergence and raising of the young, the arctic fox occupies a permanent territory sometimes demarcated between natural boundaries in the form of streams, knolls and other particular relief features. In the event that a “foreign” arctic fox intrudes, it is repelled by the parents; in this case, even the weakest female can drive away the stronger newcomer. However, the area does offer complete security to the whole family, as the parents go for food to the seashore or to other regions (Cherskii, 1919–1920; Boitsov, 1937; Barabash-Nikiforov, 1939). Thus, the home range is as much a breeding as it is a feeding territory.

The dimensions of the selected territory vary according to the locality and abundance of food. In rugged terrain, the areas are smaller than on the plains. In the delta of Lena, the area inhabited by a family in the summer is from 5 to 30 km². In the northern part of the Kharaulakh range, dispersal of the arctic fox from the burrow in June 1927 did not exceed 5 km; the same was also observed on the plains in the lower Anabara river in 1934. Both years were characterized by low numbers of lemmings. On the Taimyr, in the region of Ozhidanie bay, in the year of a good “yield” of arctic foxes (1947), the area of their breeding territory comprised not less than 16–25 km²: 3 burrows with litters were found at a distance of 4–5 km from each other (A. Romanov, 1941; Sdobnikov, 1958). Breeding territory on the Kanin, defined as the distance between burrows, was equal to 2–14 km², sometimes more in North Yamal—up to 25–30 km², and in the Lena-Khatanga territory—from 20 km² and more. On the Bol'shezemel'sk

and Malozemel'sk tundras, in 7 centers of arctic fox concentration in an enormous territory of 16,500 km², in a comprehensive tally each 2 km² contained only one burrow on the average (Skrobov, 1958). With food abundance and dependability, litters of these animals are sometimes placed in immediate proximity to each other, as was observed on the Yamal, Kanin, and in Belyi and Mednyi islands (Iokhel'son, 1898; Freiberg, 1926, 1939; Tyulin, 1938; Tsetsevinskii, 1940; A. Romanov, 1941; Shibanov, 1951; Sdobnikov, 1958; Skrobov, 1958; N.N. Spitsyn).

As soon as the young emerge on the surface, arctic foxes often roam from one burrow to another, especially if they are disturbed. On the Commanders, parents accompany the young to the seashore to temporary shelters (Cherskii, 1919–1920; Barabash-Nikiforov, 1937a; Maksimov, 1959).

After the young arctic foxes establish themselves at the end of summer and beginning of autumn, the boundaries of the littering sites cease to exist. At this time, the arctic fox commences a nomadic life. The distribution of arctic foxes after that depends on the abundance of food in autumn–winter period. In the years with bad supply of
 225 food, the arctic fox moves for some hundreds, thousands and even more kilometers. In years of lemming abundance in continental tundras, arctic foxes in summer restrict themselves to region of summer denning during winter also, and their individual ranges at time are not large. In the Lena delta in a year of lemming mortality, arctic foxes which remained to winter in the tundra moved for a distance of up to 10 km in the direction of baited traps (Freiberg, 1939; A. Romanov, 1941).

In the Bering and Solovetski islands, constancy of occupation from year to year of different places by definite groups of arctic foxes distinguished by their fur color and behavior was noted.

Burrows and shelters. The choice of a place for construction of the burrow, and then its use for many years, depend on many factors. Chief are the dryness of the soil and the absence of proximate subsoil water and permafrost, slope exposure, the lookout possibilities of the place, and food supply in summer time. Arctic foxes' burrows are usually located on elevated dry interfluves, on small hills, precipices, etc.

In the mountains or in outcrops of bedrock, the arctic fox digs a burrow in a fine-grained layer, and if it is absent, they settle in rock clefts and between plates of montane bedrock. On Kil'din Island,

burrows and dens of arctic foxes are concentrated in a coastal belt 1–2 km in width or narrower; here arctic foxes live at various altitudes, from some tens of meters above the water to the extreme tops of the plateau. Burrows, dug in sand, were abandoned because of frequent human visitation and their destruction, and the foxes burrowed within rocky areas under plates of bedrock (Formozov, 1929).

The arctic fox also uses the burrows of other animals, for example, the marmot [*Marmota camtschatica*] (Kharaulakh range; V.I. Kapitonov). In Magadan district, it burrows in places with old ground squirrel colonies with softer, drier soil (Shustov, Belozorov, 1959). In seabird colonies on Novaya Zemlya, arctic foxes dig burrows in the guano (Nosilov, 1909).

In tundras where wind force is great, sheltering the burrow from it is important. In the northeastern Bol'shezemel'sk tundra, burrows are more often placed at a height of 2/3 up the slope, not exceeding 12 m above water level of the nearest water body. In such a place, wind force near the burrows is reduced by 32% of its force on the slope crest (Danilov, 1958). In the zones of open tundras in the northern belt, the arctic fox prefers south slopes, without deep snowy faces, which thaw out earlier in spring, and which are protected from northerly wind in summer time. In the Bol'shezemel'sk and Malozemel'sk tundras, of the 483 burrows inspected, 26.5% were located on the southern side, 17.8% on the eastern, 14.3% on the southwestern and 11.3% on the northern side. To the north and near to the coast, the number of burrows on south slopes increases. Thus, in maritime tundra of the Taimyr peninsula, almost all burrows are located on slopes of southern exposure, while in the upper reaches of the Khantaiki, Kureiki and Kotuya rivers below 67°30' and 68° N. Lat., arctic fox burrows are restricted to the northern slopes (N. Naumov, 1934; Sdobnikov, 1958; Skrobov, 1958).

Burrows are constructed in the vicinity of water bodies, usually within 100–500 m. Paths lead to the water. In the southern zone, burrows are located near growths of shrubs in which young arctic foxes hide from enemies and bad weather, and where they can also find food in the form of ptarmigan and small rodents.

The arctic fox constructs permanent dwellings, usually in sandy and sandy loam soils, more rarely in sandy-gravel mixed with pebbles and still more rarely in clay soil. In summer, the soil temperature in burrows is some degrees higher than outside. However, Middendorf (1869) encountered in the Taimyr peninsula burrows in which even

in the middle of summer, icicles hung like stalactites, with arctic fox wool frozen to them.

226 The arctic fox digs burrows of no great depth, from 0.5 to 1 m, rarely more. On Belyi Island, in the Taimyr and in the Lena-Khatanga territory, they are distributed 10–100 cm above the permafrost (Tyulin, 1938; A. Romanov, 1941; Sdobnikov, 1958). In places with burrows, as compared to neighboring areas, the level of permafrost is lower. At Cape Osten-Saken on the northwestern shore of the Taimyr, in a place where burrows are found, the permafrost level is restricted to a depth of 65 cm (bottom of burrow to 55 cm), while to the side of the burrow, [frost] depth is 25 cm.

Complexity of the burrow increases through use from year to year. As a result of quite rapid breakdown of burrows, arctic foxes build new passages and the center of the lair gradually shifts. The breakdown proceeds as a result of settling of friable soils through constant digging; this is also favored by exposure to the air and trampling of the burrow by reindeer herds attracted thence by succulent vegetation, and also by the digging of humans. The more favorable place the burrow is located, the more often it is inhabited by a breeding pair. For that, arctic foxes each time undertake a cleaning of the holes and exit passages. Usually, arctic foxes renew 5–10 passages 2–8 m in length. In Bol'shezemel'sk and Malozemel'sk tundras, out of 483 burrows inspected, temporary burrows constituted 5.6%; 47.3% were recently dug and had from 2 to 10 exits; 29% of the burrows were of medium age and had from 11 to 25 exits and 18.1% had from 26 to 80 exits; these old burrows were, presumably, dug decades ago. More than 70 exits in one burrow are known in Kanin, up to 60 in Lena-Khatanga territory, up to 40 in the Commander islands and up to 30, in the north of the Taimyr peninsula. It happens that two or more families may occupy one burrow. On the Commander islands, arctic foxes inhabited one burrow for 15–20 years (Cherskii, 1919–1920; A. Romanov, 1941; Il'ina, 1949–1950; Sdobnikov, 1958; Skrobov, 1958; Maksimov, 1959).

In level places, or among low hills, the area of intercommunicating passages, representing a whole burrow system not rarely occupies a territory of 100–200, and sometimes 500 m². On Belyi Island, burrows were found in the form of systems of communicated passages with 53 exits occupying 1800 m²; during the year of this observation, 11 exits were made. Along the Tiutei river in Yamal, more than 10 burrows were close to each other. On Belyi Island, in

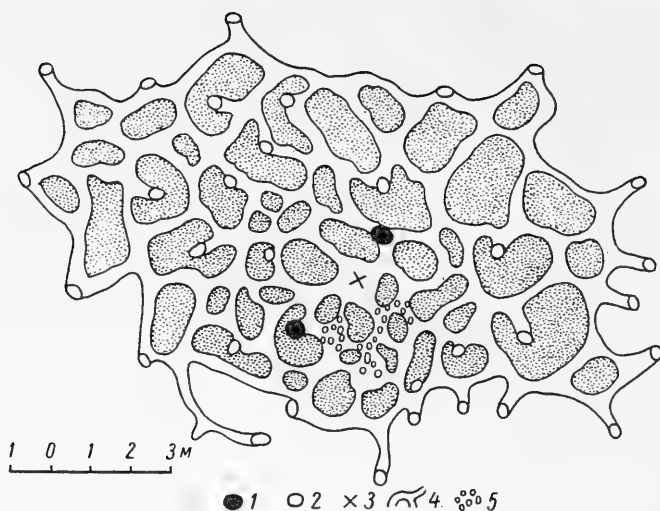


Fig. 86. Scheme of the construction of an old arctic fox burrow (from A. Romanov, 1941).

1—primary holes, 2—secondary holes, 3—nest, 4—underground passages, 5—latrine.

an area of 3500 m², 8 burrows were found. On Wrangel' island, the colonies of arctic fox occupy entire sandy hills and are riddled with countless passages (Mineev, 1935; Tyulin, 1938; N.N. Spitsyn).

227 In old burrow systems, arctic foxes make passages in 2–3 galleries with some chambers for nests. The den in which the nest is placed is lined with dry grasses and moss. The size of the nest chamber is from 0.5 to 1 m in diameter and 30–50 cm in height. The diameter of the exit opening of burrow ranges from 15–30 cm, rarely more, reaching in particular cases 80 cm. The cross section of the underground passages is 12–20 cm in height and 15–30 cm in width. As a rule, the horizontal cross section of the passages and the exits somewhat exceeds the vertical (Cherskii, 1919–1920; Boitsov, 1937; Tyulin, 1938; Dubrovskii, 1940; Chirkova, 1940; A. Romanov, 1941).

The area occupied by the burrows, the underground passages and dens are very dirty because of the remains of food and excrement. As a result of plentiful manuring of the soil with feces and remains of food, rich dense dark green vegetation, up to 0.75 m high (in Kola peninsula) develops. Plant formations on the burrows are highly variable and represent a type of northern herbaceous vegetation. In such "arctic fox meadow gardens", tens of higher plant species grow which

are absent in the majority of tundra associations. Dandelion, polar poppy, Alpine forget-me-not, and foxtail grow in Taimyr below the latitude 75° N. Lat. Near the entrances to burrows mosses (*Mnium*, *Drepanocladus*) grow. Burrows that were occupied by arctic foxes in previous years are characterized by camomile [*Matricaria*], meadow bluegrass [*Poa pratensis*] and others, or by dense herbaceous growth mixed with fire-weed and bistort. On abandoned burrows, often only short fescue [*Festuca supina*] is found (Dubrovskii, 1937; Zolotov, 1940; Sdobnikov, 1958; Maksimov, 1959). From a distance, it is easy to determine the location of burrows, which is evident in level tundra from 0.5 km, and with binoculars, up to 1.5 km. From aircraft, burrows can be seen well from a height of 400–500 m; and from 1000 m, it is possible to map a majority of centers of arctic fox burrows (Zolotov, 1940; Freiberg, 1940; A.F. Chirkova).

In winter, in periods of continuous snow storms, arctic fox makes burrows for shelter from driving snow on lee sides. The entrance is blocked by the blowing snow and the animal remains in the burrow until clear weather returns. Snow burrows are not longer than 1–1.5 m, widening at the end, of dimensions [width] 25–40 cm and height, 25 cm. The arctic fox also builds temporary burrows near food accumulations thrown up by the sea (Nosilov, 1909; A. Romanov, 1941 and others).

In years of massive reproduction, when all littering burrows are occupied, arctic foxes carry the pups outside the burrows—somewhere under the shelter of grasses, where they stay under cover of grasses, in a pile of flotsam, or even in the hollow of a large trunk of the latter (Romanov, 1941).

Daily activity and behavior. The arctic fox is active at any time of the twenty-four hour period. Scarcity and variability in the food supply force the animal to wander widely in search of food. In autumn and in winter, the arctic fox feeds mainly at night; in spring and in summer, apparently, in connection with the beginning of breeding and the appearance of their young—during the whole 24 hours. The arctic fox frequently rests in midday; in clear, windless weather, it settles down anywhere on a tussock, hillock or slope protected from the wind, on ice-hummocks or it buries itself in a snow-drift. In spring, and in the first period after the (re)appearance of the sun, the animal lies by a dark cliff or on a precipice where it is well warmed. In the Lena-Khatanga region, a female arctic fox rested in June after eating from 15:00 to 17:00 during the day and after that from 21:30 in the

evening; a male, in October arose from rest at about 06:00 in the morning and retired again at 14:30. On Mednyi Island, in good weather in the middle of June, a whole family of arctic foxes may be seen near the burrow early in the morning and again after 17:00 (Cherskii, 1919–1920; A. Romanov, 1941).

While sleeping, the arctic fox rolls itself into a ball, buries the nose in the base of the tail and covers the belly and limbs with the tail. Arctic foxes sleep deeply; during periods of noise—wind or ice-motion—it may be caught by hand (Mikhel', 1937; Rutilevskii, 1939). This is easily done during times of hunger, when the arctic fox is seriously weakened.

The arctic fox is less sensitive to fluctuations in temperature than red and corsac foxes, as a result of which, at positive [above-freezing] temperature, the general activity of the arctic fox is less than at
 228 negative. By lowering of temperature from $+15^{\circ}$ to $+5^{\circ}\text{C}$, the frequency of breathing of the white fox is increased. In the blue fox, within the limits of $0\text{--}30^{\circ}\text{C}$, such dependence is not observed. Gas exchange and heat production are greater in summer and less in winter. Daily heat production for 1 kg body weight is 450 kilojoules⁵¹, in autumn, it is higher and in spring and especially in summer, it is still higher, reaching 579 kilojoules (Kalabukhov and Poluzadova, 1946; Kalabukhov, 1950; Pozdnyakov, 1953).

In spring and summer, arctic foxes are most active on the quiet, cloudy days and in warm weather, with light wind. On cold windy days, and especially during heavy rain, its activity is sharply reduced, and the animal conceals itself in a comfortable place. In winter, arctic foxes do not go out during strong snowstorms, in freezing weather with severe wind, and on dark nights. On the contrary, they are highly active on clear moonlit nights, during northern lights and at dawn. Arctic foxes do not react to light wind, but in a strong one they move into it. Upon encountering wind, they come to a halt, most commonly in mild weather. On Belyi Island, they fall in traps usually in calm weather and during weak and moderate wind speed of 6–7 m/second. On the Chukotka peninsula, arctic foxes, on the contrary, are more active and incautious during violent snowstorms and frequent inspection of the traps at this time yields a large catch (Freiberg, 1934; Dubrovskii, 1937; Tyulin, 1938; Shundik, 1948; Yanygin, 1948; Sdobnikov, 1958). On the Solovetsk islands, up to 50% of the arctic

⁵¹According to international system of units (IS).

foxes go seeking for food at a right angle to the wind, up to 40% go with the wind and only 10% go against the wind (Boitsov, 1927). The same is observed on the Murmansk coast.

As compared to the red foxes, the arctic fox is bold and more trusting. Steller (1774) mentions how "innumerable packs" of arctic foxes surrounded a camp of people and became each day "more courageous and mischievous". The arctic foxes strewed about not only provisions which were even stored in barrels but also invaded people's living sites, chewed and dragged off clothing, shoes, and instruments. During his journey south from latitude 85° N. Lat., F. Nansen (1897) was also subjected to "attack" by a great number of arctic foxes which strewed about his belongings. Now, arctic foxes are significantly more cautious. Nevertheless, factory workers in Yamal, Taimyr and others have more than once reported the pillage of the meat and fish stores and other products by arctic foxes. When an arctic fox is driven with reindeer, the exhausted animal hides under a fur thrown on the snow. Arctic foxes on Ushishir Island are very unwary (Kuril chain; Klumov, 1960).

Mousing animals and also migrating arctic foxes frequently notice humans only at a distance of several meters. In this case, the surprised animal sits down, looks at the person, sometimes stretches and then jumps up and continues on its way. On the Commander islands, where arctic foxes are protected, they inhabit villages, bringing their pups near houses or sheds. The parents, usually in turn, keep close to their litter, and after becoming accustomed to people, take the food from their hands. They may wander for hours only a few steps behind people, barking and sometimes sniffing inhabitants (Cherskii, 1919–1920).

In captivity, arctic foxes quickly become tame. Getting accustomed to humans, some arctic foxes return after being set free. In the arctic fox, conditioned reflexes are easily developed. On the Commander islands, the animals knew well, by the clock, the time of their supplemental feeding and quickly respond to a sound signal. To a whistle, accompanied by the distribution of dried salmon or fur-seal meat, "arctic foxes appeared as if from underground, ran immediately, and yelping jumped on the handout" (Barabash-Nikiforov, 1937).

The relationships of the arctic fox to various animals are diverse. Above were mentioned reindeer and polar bear. Flocks of brant geese, gulls and skuas actively repulse the attack of the predator. On the
229 Commander islands, the arctic fox drives pigs away from the flotsam,

but at the same time, it plays with tethered goats. Arctic foxes are afraid of cats and dogs, especially where people incite them. In Novaya Zemlya, arctic foxes follow dogs to carrion, and sometimes, especially the young, play with them and even with humans (Shrenk, 1855; Nosilov, 1909; Cherskii, 1919–1920).

On a level surface, a dog can easily catch the arctic fox, but in hilly or tussocky places or in ice hummocks, the arctic fox runs away from it. The manner of the arctic fox is similar to that of the corsac fox; it runs in zigzag with sudden sharp turns; it confuses dogs.

In catching lemmings, the arctic fox waits for a long time for the appearance of a rodent from a burrow, then jumps and crushes it. Listening to the squeak or rustle of a lemming, the arctic fox can in a few seconds excavate the snow to a depth of 1/2 m or more. While hunting for lemmings, the arctic fox can easily come within gunshot of a man. A case is known of an arctic fox which, while digging up small rodents during a snow storm, was caught by a hunter by the tail. On seeing a gull on a rock on the shore from a distance of 120 meters, an arctic fox not yet molted went on with slow steps, confining itself to patches of snow; at 15–18 m, it lay and crept on its belly, and then with a strong jump caught the gull (Chastin, 1939). At the molting time of geese, arctic foxes hunt them communally, driving the helpless bird to their comrades; the arctic fox throws the captured goose on its back and pulls it. It drinks the eggs of large birds through holes made by the canines.

On the Commander islands, wandering constantly among the hauling places of fur seals, arctic foxes search for not only dead animals, but also pull away the young fur seals from lone females holding them by a unique method, by the lips; they take mainly the sick and weak (Barabash-Nikiforov, 1937).

The arctic fox eats part of a large prey on the spot, and carries the remainder to a burrow or buries it. In years with abundant food, the arctic fox makes a store, collecting some lemmings, fish or large birds; it buries their bodies in the ground or in sand, firmly tamping the surface with its nose; it pushes them under stones, ice blocks and so on. A case is known on Mednyi Island when arctic foxes took about hundred eggs from the tin box of some sleeping hunters, burying the greater portion in a *laida*. On the same island, they observed the return of arctic foxes to their stores to eat them (Cherskii, 1919–1920). All the same, a great portion of the hidden food is not utilized by arctic foxes.

The behavior of the arctic fox changes in various years depending on the abundance of food, prevalent weather and other reasons. With abundance of lemmings, white hares and willow ptarmigan, the arctic fox in the Bol'shezemel'sk tundra wanders little, and restricts itself the whole winter in proximity to its burrows, frequently hiding in them. When feeding on a second grade food [source], arctic foxes behave uncomfortably, but nonetheless do not leave summer habitats. In case of food deficiency, the animals go to the seashore or migrate in other directions (Skrobov and Kozhevin, 1957). In years of famine, arctic foxes move close to the winter stations and villages, lose their prudence and even defend their prey against humans (Commander islands, Tomsk district) (Cherskii, 1919–1920; Likhachev, 1930).

The arctic fox takes to water and during migration they swim across large lakes and rivers, for example, the lower Taimyr, 400 m in width and a current velocity of 3.5 m/s. They swim across the lower Khatanga (1–1.5 km) as well as Yenisei and Ob', straits in the Bol'shezemel'sk tundra (2 km wide) and to Kil'din Island (Tret'yakov, 1871; Formozov, 1929; Rutilevskii, 1939; Shastin, 1939; Chirkova, 1955 and others). In Alaska, the arctic fox has mastered straits up to 4 km wide.

The speed of the arctic fox in water is 2–2.5 km/h, slower than in the dog. While swimming, the animal holds its back and tail above water, the latter at a small angle. When the tail gets wet, indicating fatigue, the fox quickly drowns (Shastin, 1939). The arctic fox swims also across rivers containing slush at water temperature of about 0°C; on being turned around several times in a whirlpool, the arctic fox
 230 does not become disoriented and swims in a defined direction. On coming out on shore, it shakes itself and immediately runs rapidly away from the shore.

At the beginning of migration, masses of arctic foxes gather by rivers and run at the very edge of the water (see also p. 330). As long as ice is smooth, arctic foxes gather on the lakes, playing and harrying one another. At the sound or sight of an airplane flying at a height of 100–200 m, the arctic fox takes a defensive pose and lies on its back (V.P. Makridin); at such a time, the red fox runs away.

On the Commander and Solovetskii islands, according to the behavior and hunting habits, arctic foxes are divisible into the following groups: 1) Sedentary animals, leading an inactive way of life, and living in permanent places near human settlements, chiefly by scavenging; 2) half-sedentary animals, carrying on in a region of permanent

habitation, but sometimes moving to places inhabited by neighboring groups; 3) wandering arctic foxes. On Mednyi Island, the more alert and active are the tundra arctic foxes who hold aloof from people. On the Solovetskii Islands, vagrancy is developed mainly among males. The predominance of males among the migrating animals is, apparently, characteristic of arctic foxes of the mainland tundras (Barabash-Nikiforov, 1937a; Boitsov, 1937; Chirkova et al., 1959).

The behavior of the arctic fox varies sharply with the beginning of the reproductive period (Cherskii, 1919–1920; Barabash-Nikiforov, 1937a; Boitsov, 1937; Chastin, 1939; A. Romanov, 1941 and others). On Mednyi Island, the premating roll-call among males starts early in January. At night in February, the plaintive howling, yelping, and squealing of females are heard. In March males frequently urinate near burrows and feeding places; females urinate, raising the tail, and allowing males to approach them. The animals run, often holding something in their teeth—a bone, stick or lump of snow. Playing between mated pairs alternates with hard fights among males. In the location of the fight, bits of wool, and sometimes blood are left; on Mednyi Island, it was observed that at that time, arctic foxes injure the genital organs of each other. In fights, up to ten animals are involved. In the northern Taimyr peninsula, nuptial games were observed on 20 April 1936. The mating of arctic foxes is accompanied by loud screeches.

In some instances, male and female become strongly attached to each other in the breeding period. On Mednyi Island, a female which had been taken from her chosen male and kept in an open-air cage with another male, lived with him the whole spring, but did not mate with him. During the same period, she always expressed her attention to the first male, who sometimes passed by. The latter, although he had his own mate, brought food to the caged female.

During pregnancy the males constantly offer food to their females and with special diligence not long before the appearance of the newborn. On Mednyi Island, a male carried fish "*myagon'ku*" (*Cyclopterichthys venticosus*) to a female that happened to fall captive.

Shortly before parturition, the behavior of a captured female becomes more quiet and cautious. With the appearance of the babies, both parents feed the young in turn, bringing them food and playing with them, but most often the mother remains near the burrow to guard the litter. In case of danger, the female sometimes hides in the burrows together with the young while the male strives to drive away

the person, howling and gradually moving away from the litter. In the absence of adults, the young allow a human to approach within several paces, and even after fleeing to the burrow, they appear again after a few minutes. At the age of 3–4 weeks, the animals leave the burrow, on Mednyi Island already at the end of June and the middle–end of July, they start playing independently. Making excursions, they frequently change burrows. At this time, their barking is first heard. In Lena-Khatanga territory, the young arctic foxes start to play within 5 days after leaving the burrow, and within 10 days, they attempt to catch lemmings and excavate their burrows and begin to feed on meat. At the age of 1.5 months, they shift over to meat and
 231 other food. In the second half of July, they share with their parents in hunting molting geese. The mother feeds the young on milk for one to 2.5 months. 2.5–3 months after birth of the young, the father abandons the litter. At the end of their life together, the mother also leaves the litter for a whole day. After the female finally abandons the young, the litter breaks up. A case is known when, after the death of the father of one litter, the mother transferred the young to the burrow of another arctic fox, where both mothers fed the young together (Il'ina, 1949–1950).

The more the year is deficient in food, the longer the time taken by the parents in search for food, and the earlier they leave the young. With food abundance, members of the family stay together until autumn, and separate gradually; individual arctic foxes live near burrows throughout the entire winter. In the former Kolymsk region, a female was found in a burrow together with her adult offspring, even in winter (Iokhel'son, 1898).

Seasonal migrations and transgressions. The arctic fox is a typical migrant, and wandering is of great significance in its life. The migration of arctic foxes must be understood as a historically established phenomenon. If judged by Pleistocene–Holocene remains, this phenomenon has existed for many thousands of years (Tugarinov, 1927; Gromov, 1928; Kirillov, 1950; Pidoplichko, 1951; Vereshchagin, 1953, 1959, 1960; Serzhanin, 1961).

The reason and stimulus for commencement of migration is insufficient food. This is confirmed by the appearance of massive and long-distance shifts of arctic foxes in years of the disappearance of the main food—lemmings. At the same time, the relationship between migration and food abundance is not invariant. The start of arctic fox movement away from the denning region is sometimes observed in

the presence of food. Migration is subject to instinct. In old animals, migration is also modified by experience. One may assume that the old arctic foxes react to signals announcing the coming of famine—an early cold snap with rain and wet snow, early departure of birds, the appearance of onshore and changeable winds and, possibly, other unknown factors. It was repeatedly observed that periodic migrations of arctic foxes from places of permanent habitation are repeated after 2–4 years.

Migrations of arctic foxes start in August–September, depending upon the time when food disappears in the main breeding places. The massive movement of animals when the arctic foxes “come in crowds”, as it is said in the North, occurs in October–November.

The route of arctic foxes before the freezing period runs along the water's edge, where a trampled path is formed. At Serebryanyi [Silver] bay on the western coast of the northern island of Novaya Zemlya, the whole shore was spotted with tracks of arctic foxes in 1887 and the beaten tracks of animals from all sides met here. On the sands of the Khatanga river, in 1931, there was a path several meters wide (Nosilov, 1909; A.F. Chirkova). Part of the arctic foxes move on a wider front. In the northwestern Taimyr peninsula, arctic foxes move along in a 2–3 km deep strip along the shore. In the northeastern Bol'shezemel'sk tundra, the animals move along a front of tens of kilometers, but the majority of them are concentrated in the coastal zone of Baidaratsk bay (Kirpichnikov, 1939; Chirkova, 1955).

In separate places, either latitudinal—western or eastern—directions predominate, as in northern Arkhangel'sk district, or meridional ones, as the well-known route of the coastal arctic fox along the Yenisei river. Migrations with departure from the tundra to the forest zone are more noticeable, and early began to attract to themselves the attention of investigators. Meridional migrations are noticeable only when they are massive phenomena. In the neighborhood of Taimyr lake, the autumn migration in 1947 was in a southeastward direction; the arctic foxes swam across the lower Taimyr from the western shore (Sdobnikov, 1958).

Animals penetrate the taiga zone in great numbers, going along the valleys of large rivers or coming out onto open watersheds; from the sea coast, they move out onto the ice and to the islands of the Arctic Ocean. The arrival of arctic foxes into the forest zone is frequently preceded by the flight of snowy owls [*Nyctea scandiaca*]

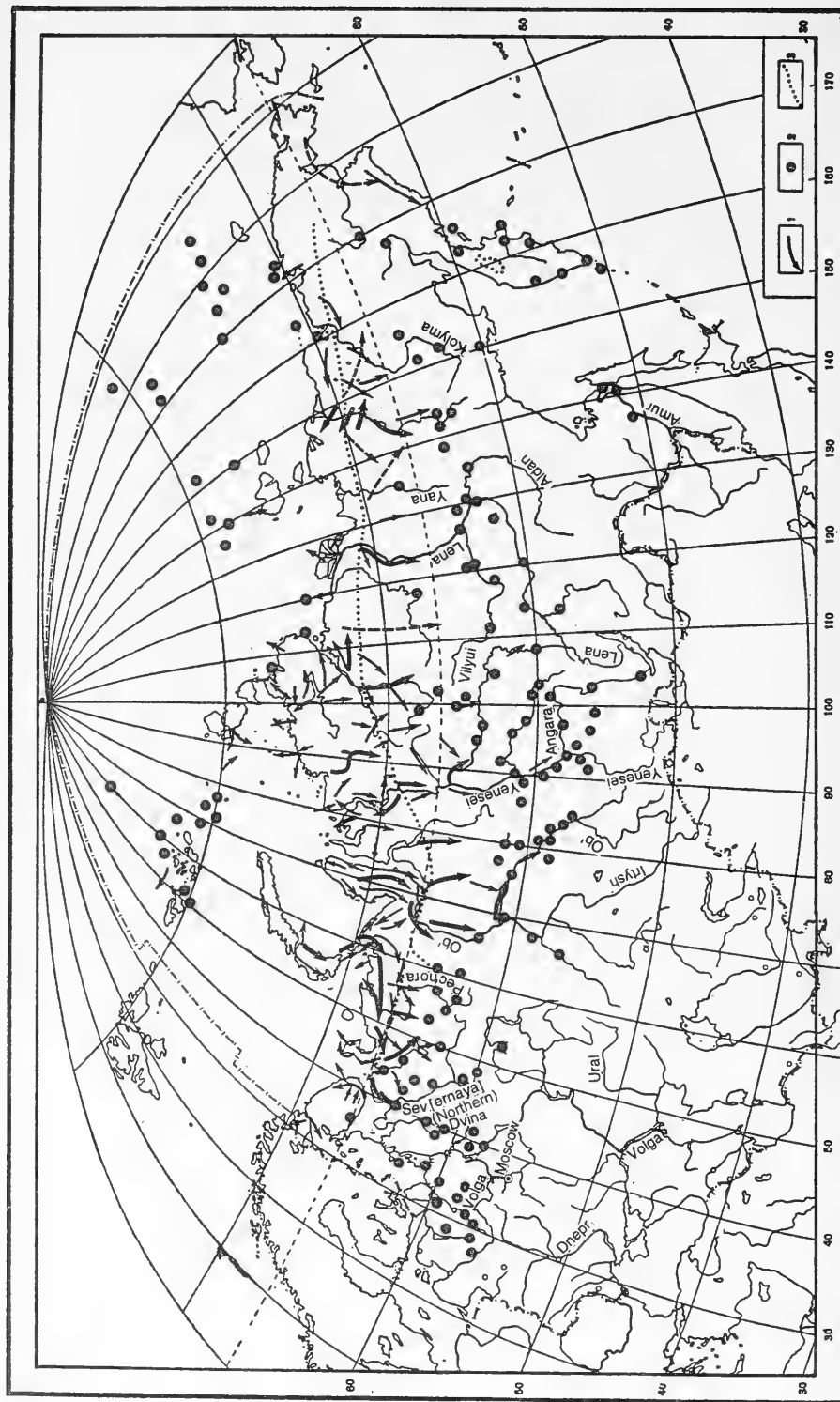
which more quickly respond to deficiency of food in the tundra and vacate it earlier.

It has been observed that arctic foxes move as though in waves. Such migrations of arctic fox groups were observed in Lena-Khatanga territory. In the interior of the Bol'shezemel'sk tundra, in 1933/34, a movement from east to west began from beyond the Polar Urals, which was noticed at the end of October when in the course of a month there was a migration of well-fed arctic foxes. After a pause at the end of December, a smaller group of animals moved, and from January 20th, during the rest of the month, individual animals were seen running by on three days. The second and third groups of animals were emaciated. On the sea coast, arctic foxes at the end of October moved the whole winter in the same western direction, the first strong wave occurring at the end of November, the next—at the end of December, and finally—in the middle of February and from the end of this month until the middle of March and later. The rut, which took place at the end of March and in April, did not stop the movement of arctic foxes, which continued running in the same direction as in winter (A. Romanov, 1941; N. Dement'ev, 1955).

In winter, arctic foxes spread out over a huge territory of tundra, forest and ice landscapes. The total area inhabited by the species increases at this time by several times and at the same time population density in the tundra decreases. The majority of arctic foxes die in unaccustomed life situations, from hunger or diseases, and are caught by hunters. Long-distance migration of arctic foxes in the majority of cases is "a way to death".

Those animals remaining alive in February–March, sometimes even in January, migrate back; in some years this extends until April and May. The first tracks of arctic foxes from the south appeared near Taimyr lake on the 20th of March, and the movement from the seashore into the depths of the tundra in 1948–1949 ended by the middle of May (Sdobnikov, 1958). Apparently, only a negligible portion of the arctic foxes return to the tundra. Individual arctic foxes remain during the warm period in uncharacteristic types of landscapes like forests and on the ocean ice.

Long-distance migrations are more often carried out by males (on the Solovetsk islands, up to 80%), but cases of long movements are also known in females, for instance in 1928, to the neighborhood of Krasnoyarsk. Long-distance movements seriously deplete arctic foxes



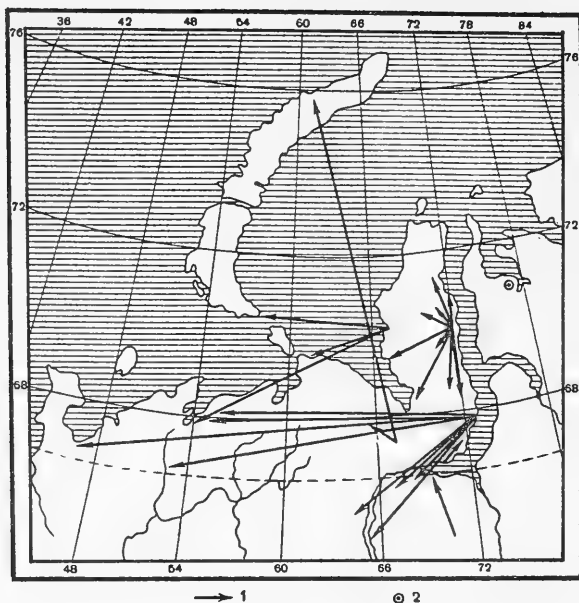
232 Fig. 87. Migration routes and long-distance movements of arctic foxes (A.F. Chirkova): 1—direction of autumn and winter migrations; 2—individual long-distance movements on the mainland in winter and encounters on ice in various times of the year; 3—southern boundaries of the breeding (denning) area on the mainland.

and suppresses their reproductive capacity (Sluchevskii, 1886; Skalon, 1928; V.K., 1929; Boitsov, 1937; Chirkova, 1955, 1959 and others).

In the forest zone, arctic foxes were observed and frequently hunted at 1000–1800 km, and in exceptional cases, 2000 km (for example near Komsomol'-na-Amur), and in the Arctic Ocean, at 1000 km from the limits of summer habitation. The average daily route encompassed by the animal is, apparently, about 20–30 km.

- 234 At the end of the 1930's, 172 arctic foxes were marked in the Novyi Port region on Yamal, of which 31 animals were re-captured (Sdobnikov, 1940; Fig. 88). A maximum translocation of about 1200 km in a straight line as it went across ocean ice to the north island of Novaya Zemlya, was made by one animal. The majority of arctic foxes moved off in a southwesterly direction; the farthest ones were caught near the village of Muzhi on the Ob', at the mouth of the Pechora, at the Snopa river on Chesh Bay, at the southern end of Novaya Zemlya, and at its northern limit.

When food decreases in years of the animal's abundance, almost all arctic foxes migrate or disperse to different areas away from their denning places. Districts to which they dispersed to the south for the majority of migrating arctic foxes were to be found in the northern subzone of the forest. When a peak of migration is reached along a permanent route, one may observe large numbers of foxes. Thus, in 1887 during one stroll on the western shore of Novaya Zemlya, Nosilov (1909) encountered hundreds of animals, and in the course of two weeks in October, by his estimate thousands of foxes passed by. After migration to the southern island, only single individuals remained. On the southern coast of Belyi Island at the end of September 1930, tens of foxes were seen, through binoculars, wandering about awaiting the formation of fast ice (A.F. Chirkova). On Dikson Island, on good "movement" days 5–6 arctic foxes were seen directly in a distance of 1 km (Heptner, 1936). On the lower Taimyr river, between 18 and 20 September 1935, each day up to 21 foxes swam across while on September 1947, 10 to 15 foxes were observed at one time within a radius of 2 km in this region (Sdobnikov, 1958). On the Chelyusk peninsula, during the time of the arctic foxes passing at the end of October, one might see at one time up to 46 animals, after which the number dropped sharply; during winter, there were only separate individuals. The total number of foxes that passed through an area of 10 km in autumn 1932 constituted not less than 1500 to 2000 individuals, and in spring, during the period of their return,



233 Fig. 88. Directions and limits of migrations of individual arctic foxes marked on Yamal (from Sdobnikov, 1940): 1—direction of movements; 2—no movements.

there were not less than 800 (Rutilevskii, 1939). On the right bank of the lower Khatanga, upstream from Cape Bol'shaya Korga, tens of passing arctic foxes were counted each day on 24 and 25 August 1931. Along the left bank of this river near the mouth of the Novaya river, from 2 to 80 fresh tracks of arctic foxes were noted on a 10-km route at the beginning of October, and below Khatangsk village, it was possible to observe 2 to 4 migrating arctic foxes at one time at any time of day starting from September 17; after ice formation on October 10, arctic foxes disappeared. In that period, no less than 1000 animals passed by Khatangsk village (A.F. Chirkova).

In Arkhangel'sk district, judging by the number of prepared skins, the number of arctic foxes emigrating for long distances only in a south and southwestern direction constituted, in some years, about 10, 20, or 30%. No less than this number of arctic foxes departed to the north across the ocean ice. In this manner, during years of extensive migration up to 2/3 of all arctic foxes abandon the tundra zone.

At the time of massive movements, the behavior of arctic foxes changes. At the beginning of migration, the direction of movement of

individual animals is variable, undefined and might be directly opposite one another. In this time, arctic foxes wander nervously and swim across rivers and canals. Coming to the banks of large and as yet unfrozen rivers, groups of arctic foxes start to change direction along them, running along the sea coasts and along mountain ranges and valleys; they move in response to the density and depth of snow cover, the weather, especially winds, and also to the availability of food along the way.

At the beginning of migration, arctic foxes move in pre-twilight or early morning accustoming themselves to the trails trodden by previous confreres; without looking aside they hurriedly overcome the difficulties along the way. Later arctic foxes energetically run, trot or even gallop day and night, with this frequently barking or howling. Being distracted for a short time to search for food, their hunger barely satisfied, the animals again start on their predetermined way.

On clear moonlit nights or during the period of the northern lights [aurora borealis], active movement is initiated. On their route, the arctic foxes move through villages, especially at night, and it is only during the light part of the 24-hour period, when people and dogs are present on the shore that the animals detour or lie in wait for the
 235 departure of people. Their instinct for wandering is so strong that the animals may stop for some time only to spread out at the beginning of migration to feed up, although the animals still remain in the denning region or have only started to migrate. During the peak of their movement, hunting for food detains the animals only briefly.

Arctic foxes from different geographic populations may sometimes mix during migration. Thus, in the winter of 1956/57, in a year of migration from the east, an average of 50% of the arctic foxes captured in the vicinity of Kara at the very edge of the Bol'shezemel'sk and Yamal tundras were related by their fur to the Obdorsk type, characteristic of the Yamal foxes. In the western Bol'shezemel'sk tundra, such animals constituted 30%, and on the Kanin peninsula, less than 10%; all those remaining were referable to the local Pechora type characteristic of the European north (Chirkova et al., 1959; Fig. 82).

Reddening of the fur⁵² that is observed in arctic foxes and other carnivores on the underside of the paws, rarely in the axillary

⁵²In microscopic view, the reddish color stains equally every hair. The color is not soluble either in water or in soap, and it resists the action of alcohol, ether, chloroform, xylol and hydrogen peroxide (Chirkova et al., 1959; Shilyaeva, 1961; A.I. Solntsev).

depressions and on the belly, is obviously caused by skin gland secretions connected with periods of great stress on the organism, and appears particularly intensely during the time of the animal's migration. Thus during the extensive migration of arctic foxes in the northeastern Bol'shezemel'sk tundra in the autumn and winter of 1951/1956, the reddening of the fur of the foot pads and between the toes was noted in approximately half of the arctic foxes captured in the Kara region (42% bright color). In the following year during the absence of migration, reddening of the paw fur was only noted in a small number of animals (2% bright color in all) (Chirkova et al., 1959).

Basic migration routes and long-distance movements of arctic foxes are known over a large part of the species' range (Fig. 87). On the Kola peninsula, the arctic fox migrates mainly along the valleys of Kamenka, Kochkovka, and other rivers, [flowing] from the interior of the peninsula to the sea. From the northwestern Kola peninsula it runs southward to Murmansk and farther, along the railway line.

Rare cases of the appearance of individual foxes were observed in the territory of the Lapland preserve and on the Tersk shore in the Olenitsa and Kuzomen' regions (Ozeretskivskii, 1904; Dubrovskii, 1939; Zolotov, 1904; Nasimovich et al., 1948; Drebensov, 1959).

After the formation of fast shore ice and the appearance of ice at the mouth [entrance]* of the White Sea, the arctic fox moves off to the Kanin side, from whence they return in March, before the start of ice breakup. The large exodus of the arctic fox is repeated every 4 to 6 years. The emigration of arctic foxes to the Varanger Fiord side, and the event of their appearance in northwestern Finland near Enontekiö is notable (Kleemola [and] Laine, 1961).

Counter-movements across a wide distance take place in the European north, to the east of the White Sea, from the northeast to the southwest and west through the Bol'shezemel'sk, Malozemel'sk and Timansk tundras (Folitarek and Chirkova, 1930; Sergeev, 1934; A. Korsakov, 1941; G. Naumov, 1941; Maksimov, 1945; Chirkova, 1955). Arctic foxes skirt to the south of Chesh, cut across the Kanin peninsula or follow around it, turning to the north along the eastern shore, and drop down to the south along the western; they migrate along the Zimnii coast of the White Sea to Dvina Bay. The arctic fox

*The Russian word used is *gorla*, meaning throat—Sci. Ed.

frequently crosses the lower Pechora and other large rivers in specific places.

Many arctic foxes migrate southwards along the Pechora, Mezena, Pinega, Northern Dvina, Onega rivers and their tributaries to the upper Vychegda, Sukhona, Yuga and others. The most extensive emigrations of the arctic fox, up to 58–56° N. Lat., were known even in the past century, and also in the present century in southeastern Latvian SSR, in Pskov, Novgorod, Leningrad, Kalinin, Vologda and
 236 Kostroma districts, and in the northwest and east of the Kirov district. Migrations were noted as far as the vicinity of Troitsko-Pechorsk village and the mouth of the Ilych river, and also in Ust' Kulomsk, former Storozhevsk and Letskii regions (60° N. Lat.) of the Komi ASSR (Middendorf, 1869; Sluchevskii, 1886; Dmitrieva-Sulima, 1911; Paramonov, 1929; Ognev, 1931; Lavrov, 1932, Sergeev, 1934; Guber, 1937; Ostroumov, 1949; S.V. Shibanov, A.F. Chirkova).

In the Pechoro-Ilych preserve, arctic foxes during the period from 1929 to 1949 appeared in the course of 9 winters: in 1929/30, 1935/36 and 1937/38 there were massive migrations, and in 1933/34, 1938/39, and in the course of four winters from 1944/45 to 1947/48, individual animals were encountered. Apparently, movement of the arctic fox on the territory of the preserve was limited by the depth of snow cover; in years of large transgressions, the average maximum depth of snow cover was 74 cm, but, in winters of occasional appearances—98 cm. In heavy snow years, the arctic fox often remained along rivers, moving on the ice, being malnourished and diseased (1929/30 and 1935/36). In light snow winters (1937/38) they moved freely through the taiga. There is a supposition that occasional arctic foxes, moving into the preserve in 1944–1945 continued to live there and did not depart for 4 years; after the capture of two animals in 1947/48, no more foxes were encountered (Teplov, 1960).

Some of the arctic foxes from the northeastern Bol'shezemel'sk tundra move over to Vaigach and Novaya Zemlya, across the ice of the Barents Sea, and then arrive at Kolguev [island]. The migration of arctic foxes in Novaya Zemlya was intensive in the last century along the western and eastern shores of both islands (Nosilov, 1909). Good passages of arctic foxes on Novaya Zemlya occur twice a year—in autumn and spring (Dubrovskii, 1941). In different years, arctic foxes move from Bol'shezemel'sk tundra to the Urals. Waves of massive migrations in the north of Arkhangel'sk district were noted in the winters of 1909/10, 1914, 1926/27, 1929/30, 1935/36,

1937/38, 1944/45, 1946/47, 1947/48, 1954/55, 1956/57 (Dmitrieva-Sulima, 1911; Folitarek and Chirkova, 1930; Bashkin, 1940; A. Korsakov, 1941; G. Naumov, 1941; Maksimov, 1945; Chirkova, 1955; Chirkova et al., 1959).

Basic migration routes on the Yamal peninsula, when, according to Nentsi stories, foxes run "in herds," go in a meridional direction, along the shores of Ob' Bay and the Kara Sea, and also along the central Khoi watershed. The arctic foxes move out over a wide front along the ice of the Kara Sea.

Less significant are migrations along the Taz and Pur rivers to the east on the Yenisei. The most southern places in west Siberia where arctic foxes appear are noted in the vicinity of Nyaksimvol' (63° N. Lat.); in the belt of southern taiga along the course of the Irtysh and Tobol, below Tobolsk and even Yalutorovsk (56.5° N. Lat.), below Tevriz (57.5° N. Lat.). Dispersal of foxes to the vicinity of Tom'sk (57° N. Lat.) is known (Skalon, 1928; Formozov, 1935; Andreev, 1937; Laptev, 1958; M.A. Sergeev). Long-distance movements of arctic foxes into the forest zone of west Siberia took place in 1921, and in the seasons of 1926/27, 1929/30, 1932/33, 1937/38, 1941/42, 1944/45, 1947/48, 1954/55, and less significantly in 1930/31, 1933/34, 1935/36, 1939/40, 1946/47 and later. Migrations of the arctic fox are also known in 1910 and 1913.

In northern Krasnoyarsk territory, the arctic fox takes itself upstream along the Yenisei to the mouths of Lower and even the Podkamennaya [stony] Tungusk. Occasional arctic foxes reach Krasnoyarsk (V.K., 1929, and others), the upper course of Lower and Podkamennaya Tungusk (60° N. Lat.), to the region of the city of Bratsk, even the villages of Aban and Taishet along the main Trans-Siberian railway ($56-57^{\circ}$ N. Lat.). From the Taimyr peninsula, large numbers of arctic foxes migrate along the Pyasina and Nizhnaya Taimyr rivers and also along the shore of Taimyr lake, departing from the tundra zone through the belt of northern taiga forest to the Central Siberian Plateau. A well-defined migration of arctic foxes takes place along both shores of the Khatanga gulf and Khatanga river and its tributaries, the Popigai, Kheta and Kotui, where the arctic fox reaches the upper courses of these rivers. To the north, arctic foxes disperse across the ice to all the nearby islands, in particular Severnaya Zemlya and Vize island—at 78° N. Lat.

Large migrations and long-distance dispersal of arctic foxes in the northern Krasnoyarsk territory are known in 1860, 1913, 1922/23, 1925/26, 1927/28, 1931/32, 1935/36, 1944/45, 1946/47, 1947/48, and 1954/55 (Tret'akov, 1871; Aleksandrov, 1927; Buryakov, 1929; N. Naumov, 1930; Heptner, 1936; Shastin, 1936, 1939; L. Popov, 1939; Chirkova, 1955).

Arctic foxes in Yakutiya wander not only along the rivers but also in the interfluvial country along the Kharaulakh, Chekanovsk and other ranges. Transgressions were observed in the upper Anabar, Olenek, Vilyui, and Lena rivers (Mukhtuya and Olekminsk villages, 61° N. Lat.) and along the Vitim (Mama village, Irkutsk district, 58° N. Lat.), in the vicinity of Yakutsk and Krest-Khal'dzhai village on the Aldan. Arctic foxes were found along the Omoloi and Yana rivers to the latitude of Verkhoyansk, along Indigirka to Oimyakon village (63° N. Lat.), on the upper Kolyma to Seimchan (62.5° N. Lat.) and its tributaries, the Yasachnaya and Korkodon (Tkachenko, 1932; Tugarinov et al., 1934; Kolyushev, 1936; Guber, 1939; Skalon, 1940; Skalon et al., 1941; A. Romanov, 1941; Belyk, 1953). Extensive migrations of foxes take place here in the tundra zone and along the shores of the Laptev and East Siberian seas, in both easterly and westerly directions. Arctic foxes come to the Anabar river basin following the migration of wild reindeer herds from the eastern Taimyr.

Commonly, arctic foxes disperse across the ice of the Arctic Sea, to the New Siberian and other islands (V.U., 1935, Zarovnyaev, 1933; A. Romanov, 1941, and others). Masses of arctic foxes, together with seals and polar bears, remain in winter among the [ice] hummocks in the sea 250 to 350 km from the mouth of the Olenek river; here these animals seek their living. After strong winds and snowstorms, the arctic fox wanders back to the sea-coast (Vasipev, 1935).

Migrations of arctic foxes in the western and eastern regions of the Yakutsk ASSR do not proceed simultaneously. Large migrations of arctic foxes to the east of the Lena (along the Kolyma, Indigirka, Alazeya and others) were observed in 1895, 1903 and 1944/45; and in the western regions, in 1926/27, 1932/33, 1947/48, and 1954/55. In 1929/30 and 1935/36, long migration of arctic foxes originated, apparently, on the whole territory of Yakutiya (Iokhel'son, 1898; Buturlin, 1913, E. Sh., 1930; Tugarinov et al., 1934; Skalon, 1940; A. Romanov, 1941; Chirkova, 1955).

F. Wrangel' (1841) even saw arctic foxes on the ice of the East Siberian Sea between the Medvezhie islands and the De Long strait. Some information is available on movements of arctic foxes along the shores of Chaun bay to Wrangel' island and back at Cape Uelen, and eastward across the Bering Strait, and also in a south-western direction along the shore of the Bering Sea (Mineev, 1935; Chirkova, 1955 and other materials).

Transgressions of arctic foxes are rarely observed on Kamchatka—in the Parapol valley region on the isthmus, on the western coast to Ust'-Bol'sheretsk, the southern end of the peninsula and the northern Kuril Islands; on the eastern coast of the peninsula—to Ust'-Kamchatsk and the Kronotsk peninsula. In 1895 and 1896, several arctic foxes were caught near Petropavlovsk (Paramonov, 1929; Sergeev, 1936; Guber, 1939; Yu.V. Averin).

Arctic foxes were noted at Gizhiga and Penzhino (Ognev, 1926) and along the western shore of the Okhotsk Sea (Sergeev, 1936; Guber, 1939). Nordmann (1861) was the first to point out the occurrence of the arctic fox in the lower Amur. Later transgressions, or possibly the transporting of separate individuals on ice, were observed at 51–52° N. Lat. on the western shore of the Tatar strait, in the Ul'chsk region in the winter of 1949/50 and in the vicinity of Komsomol'sk-on-Amur in the autumn of 1958 (Belyaev, 1959).

F. Nansen encountered arctic foxes on the ocean ice below 85° 20' N. Lat. in April 1895, 300 miles from the nearest land (Franz Josef Land). Brusilov (1934) during the period of the "Northern Anny" drift [ship in ice] noted the presence of arctic foxes in the winter of 1913/14 on the ice between the islands of Novaya Zemlya, Franz Josef Land and Severnaya Zemlya, approximately from 77° to 82° N. Lat. and from 60° to 80° E. Long. De Long (1936) saw arctic foxes and their tracks at a latitude of 72° to 77° N. Lat. between Wrangel', Geral'd and Bennet islands. During the voyage of the ice-breaker "G. Sedov" and later on
 238 the drifting polar stations "Severnyi Polyus" [North Pole] 2, 3 and 4 in the "inaccessible pole" and other parts of the ocean, arctic foxes were found between 77°–87° 45' N. Lat. and 129° E. Long.–157° W. Long. at distances ranging from some hundreds to 1000 km to the north and northeast of the New Siberian islands (Badigin, 1940; Buinitskii, 1945, 1946; Karelin, 1945; Ostrekhin, 1945; Chapskii, 1946; Rutilevskii and Uspenskii, 1957; Kirillov, 1958). The most northern point at which the arctic fox has been observed is ~88° N. Lat., at a distance of 800 km from the nearest land—Ellesmere Land (Uspenskii, 1956). The

majority of occurrences of arctic foxes met with on ice are noted in November–December, and rarely in March–April.

In the Western Hemisphere, arctic foxes migrate also in various directions, both to the south and to the ice of the Arctic Ocean. On the eastern Atlantic coast of the North American continent, arctic foxes descend along the treeless regions significantly farther south than on the western Pacific [coast]. Up to 90% of the arctic foxes within the arctic archipelago spend the winter on ice. Arctic foxes even disperse from Canada to Greenland.

*Reproduction*⁵³. Animals begin to reproduce at the end of the first year of their life, although they attain full maturity in the second year. Development of the reproductive organs begins with increase of the testes in autumn. In a year with unfavorable conditions, the formation of spermatozoa and their appearance in the excretory ducts in adult wild arctic foxes of Yakutiya, began in February at a testes weight of 2600 mg and more. In young 9–10-month-old males, sperm was formed a month later (N. Sokolov, 1957). Decrease in the volume and loss of elasticity of the testes in arctic foxes on farms takes place at the end of April–beginning of May when the prostate gland ceases its activity. The male produces sperm during the course of 2–3 months. The testes of arctic foxes are larger in size compared to those of red foxes and the ejaculate contains a large number of spermatozoa. Among captives, the arctic foxes with the least weight in summer but which rapidly increased in autumn, were found to be the best reproducers.

In the course of the winter, ovaries and oviducts of females in the pre-estrus condition develop earlier in adults than in young.

Ovulation of the spontaneous type does not depend on the time of mating. Before the beginning of ovulation, the ovary of the arctic fox is larger than that of the red fox, and although the ova are smaller, the number of Graafian follicles is larger; this fact determines the fertility of this species.

Estrus in arctic foxes is more prolonged than in the red fox, and on animal sovkhoz [state farms], it lasts 12–14 days, but under natural conditions the female remains [in estrus] for only 4–5 days

⁵³Middendorff, 1869; Cherskii, 1919–1920; Paramonov, 1929; Barabash-Nikiforov, 1937a; Dubrovskii, 1940; A. Romanov, 1941; Rakhmanin, 1959; Skrobov, 1958; Chirkova et al., 1959; Starkov, 1932, 1937, 1940; Tavrovskii, 1946; Il'ina, 1952 and others.

on the average. During estrus, the mammary glands enlarge to 0.5 cm in diameter. In the copulatory period, the male and female pair; on farms this may last from one minute to several (4) hours (Boitsov, 1937); coitus may occur repeatedly.

In nature, the breeding season extends from the second half of winter to the end of summer. With the appearance of the first rays of the sun, courtship behavior begins. At this time, 1–2 males, rarely more, run after one female (in captivity, 2–3). The peak of rut and mating are often observed in March—beginning of April. Adult animals commence breeding first, and then the young (on Yamal, 10–15 days later), and last are those which have returned from migration.

In various regions of the USSR, over a wide area the breeding dates of arctic foxes are nearly the same (Table 28), but the appearance of young in the northern subzones of the tundra is normally 2–3 weeks later compared to the southern (Yamal, Taimyr).

239 In one or another place, the breeding season and fertility of the arctic fox can change annually in connection with the dynamics of nutritional conditions and age composition of the populations. The mating period in one place fluctuates within 2–3.5 months, and the time of birth of young arctic foxes is shifted by 1.5–2.5 months on the continent and up to 3 months in the Commander islands. Under favorable conditions, a local concerted mass rut is observed; in a year following inadequate food, it is undetectable, prolonged, or greatly delayed. In certain years, fertilization and implantation occur in 70–80% of the females and, in some places, possibly even more. At this time all littering burrows are occupied by young, and some arctic foxes deliver their newborn under clumps of grass. In other years, the majority of females remain barren and 10–15% or less of the littering burrows are occupied (see also p. 365ff.).

After mating, arctic foxes explore the region which they have chosen, and the female begins clearing the burrows. This takes place at various times of day depending on the general course of reproduction, mainly in connection with the nutritional conditions of the year. In the Solovetsk islands, arctic foxes began to choose the place for the future nest but the burrows were ready 5–15 days before parturition. One female which was bred on 19 April, occupied a burrow together with a male on 21 May, and gave birth on 6 June. In Yamal, the burrows are also cleared from March to the beginning of April—and on Belyi Island, to 20 April. In the lower

Yenisei, already in March, a female wandered around a hillock which she chose for her future lair, making a round of up to 5 km. In the northwestern Taimyr peninsula the clearing of the burrow progressed from the second half of April, and in Lena-Khatanga territory—the middle of March; a pregnant female littered here on 7 June, and emerged after parturition on 10 June. On Mednyi island, the Arctic foxes now distribute themselves among the burrows after mating.

In captivity, gestation continues 49–56 days, 52 on the average (also confirmed by observations in nature). In the earliest and latest parturition (45th, 62nd* day), newborn often die. The abdomen obviously increases in size 1–2 weeks before pupping, sometimes earlier. The female usually whelps in a burrow, but sometimes directly at the entrance: this is often a young female that did not prepare the nest, and later, are carrying the newborn to the burrow. The duration of parturition depends upon litter size, after approximately half an hour, the first pup appears; sometimes, parturition is extended over 2–3 days. Most often, the female delivers herself of her litter** at night or early in the morning.

In the tundra, mass appearance of the newborn arctic foxes occurs in May and June and coincides with fawning of reindeer, the return of willow ptarmigan, and the arrival of geese, gulls and other birds. The earliest parturitions of arctic foxes known are mid-April on the Commander islands, the end of April on Novaya Zemlya and Belyi Island, and the very latest, in June in Severnyi (North) Yamal, Lena-Khatanga territory, Commander islands, and other places.

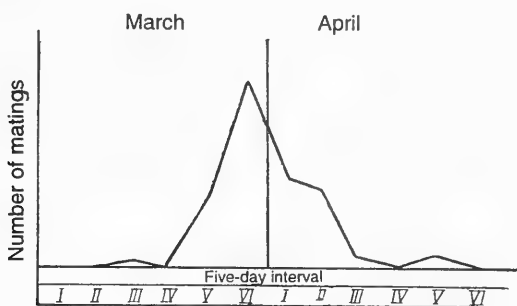


Fig. 89. Times of mating of arctic foxes in island husbandry on Kil'din, Murman (from Zolotov, 1940).

*Appears inconsistent with previous values for length of gestation—Sci. Ed.

**In Russian original, literally “burden”—Sci. Ed.

Table 28. Breeding times of arctic foxes

Regions Stage	Kola peninsula and Kil'din islands		Novaya Zemlya	Northern Arkhangel'sk district	Northwestern Siberia	Taimyr peninsula	Northern Yakutiya	Northeastern USSR with Wrangel' Island	Commander islands
Rut, estrus (from-to)	From February to end of May	From middle of February to beginning of June	From middle of February to May	From middle of February to beginning of June	From middle of February to beginning of June	From end of February to middle of April	From Febru- ary-March to end of May	From Febru- ary to end of May	From end of January to beginning of May
Mass mating	In second half of March	Middle of March-April	March, April, beginning of May	March-May	March	March	Second half of March and beginning of April	—	March
Whelping (from-to)	End of May- beginning of June	From end of April to June and, probably, beginning of July	From begin- ning of May to middle of June	From end of April to beginning June and even in July	From end of May to June- beginning of July and later	From first half of May to beginning of July	End of May, June	From middle of April to July	
Mass whelping	—	—	Second half of May- beginning of June	—	—	Second half of May to beginning of June	—	May-June	
Authors	Formozov, 1935; Dubrov- skii, 1939; Tavrovskii, 1946	Nosilov, 1909; Dub- rovskii, 1937	Shibanov, 1951; Dement'ev, 1955; Chirk- ova, 1955; Scrobov, 1958	Kolyushev, 1936; Tyluin, 1938; Guber, 1939; Dubrov- skii, 1940; Chirkova, 1941; Chirk- manin, 1959; N.N. Spitsyn	Kolyushev, 1936; Guber, 1939; Shastin, 1939; A. Romanov, 1941; Chirkova, 1941; Chirk- ova, 1955; Sdobnikov, 1958	Middendorff, 1869; Tavrov- skii, 1939; A. Romanov, 1941; Chirkova, 1941; Chirk- ova, 1955; Sdobnikov, 1958	Mineev, 1935; Chirkova, 1955	Cherskii, 1919-1920; Barabash-Niki- forov, 1937; Il'ina, 1949- 1950	

The appearance of litters near burrows was observed from the end of May until August, and more often from the second half of June to the beginning of July; it is very rare when young appear later than August. The appearance of delayed litters in August ("of a mitten" size) or when still in summer coat (*krestovatik*)* in November, is often interpreted as a second litter: Actually, the late whelping is explainable as delayed estrus or a second estrus after failure to conceive, abortion, or death of the newborn. Cases of repeated estrus in captives are known, up to 4–5 times 7–30 days after the first mating. In some years, 5–8% of the females come into estrus for a second time. Apparently, the males, in some cases, retain the capacity to mate with the female in a later period. Thus, the testes of an arctic fox from Yakutiya, taken from its family at the end of July, still contained mature sperms (N. Sokolov, 1957).

The emergence of the litters from the burrows takes place in the course of August–October, depending on nutritional conditions, and in the unfavorable years (Kara region), even in July. In years of abundant food, the litters remain near the burrows during the course of the entire autumn and winter.

Fertility of the arctic fox is very high for a carnivore. Fertility can be judged by the number of corpora lutea in the ovaries, of embryos, and of the remains of the post-partum pigmented spots [placental scars] in the uterus. The latter are retained until the beginning of proliferation of the reproductive organs prior to the next estrus, and sometimes (in starvation) to the new estrus. In 1934, when food was abundant on the Kolyma, intensive reproduction was proceeding among the arctic foxes. In 27 females studied, the number of placental scars in the winter 1943/44 was from 3 to 24 (in the majority—10, 11, 15 and 17), averaging 12.7 for each parturient female (Cha, 1953).

The situation becomes more complicated when the population decreases. Thus, in the Kara tundra, the summer of 1956 was not favorable for reproduction of arctic foxes due to the disappearance of lemmings. Out of 22 adult females investigated in the winter of 1956/57, 8 remained barren (placental scars in uterus absent); 6 females revealed from 1 to 6 ill-defined scars, and the remainder from 6 to 16 well-defined scars at the same time (in one even in the cervical region of the uterus) and up to 10 ill-defined patches

*Local word; see p. 351—Sci. Ed.

in each. The latter might have been traces of the placentae of embryos resorbed before parturition. The largest number of scars was 21. On the average in each pregnant female about 1/3 of the embryos did not live until parturition; on the average, of 10.2 embryos, only 7.1 were likely to have been born (Chirkova et al., 1959).

The greatest number of placental scars found in one arctic fox on Belyi Island was 26 (Tyulin, 1938). The possibility of one female nursing such a large number of pups has never been confirmed. Animal breeders report up to 16 newborn delivered by one mother. Cases of finding more than 20 young arctic foxes in one burrow are most frequently explained by the union of two or more litters. Thus, in the Kolymsk area, when a colony of burrows was excavated, up to 40 or more pups were found. On the Commander islands, a case was noted of two females with their pups of various ages living with a pair of parents with its own litter in one burrow. Here also, females were observed who, beside their own offspring, had 3–4 foster pups. When breeding arctic foxes in captivity, a maximum number of 22 embryos was observed, but usually a part of them was resorbed or the pups were born dead.

Geographic variation in fertility is observed between continental and maritime arctic fox populations. In continental tundras and on Novaya Zemlya, great fluctuations are observed in litter size and the proportion of infertile (unmated) females in the various years. The number of pups in a litter in the continental tundras varies from 8–12 to 20 and more⁵⁴ on the average in years with abundant food, and decreases to 3–5 in years of famine. In the maritime tundras, for example on the Kola peninsula, in northeastern Siberia, and especially on the Commander islands, the size of litters (to 10–13 pups) and the number of females participating in reproduction varies to a lesser extent from year to year. On Kil'din island, poorly nourished females produced 4–6 pups, and females nourished better than average—11–13. On the Commander islands, reduction was
242 repeatedly observed in the number of young in litters from 6–7 to 2–3 on the average in separate places—“*ukhozh*”^{*} depending upon the abundance of natural food and supplemental food. The absence of large litters is also characteristic for the island husbandry in North America and was noted in the maritime populations of arctic

⁵⁴To 22 in Yamal (Rakhmanin, 1959).

^{*}Literally, “pasturage”; in this context, foraging places—Sci. Ed.

foxes in Greenland (Lek, 1957)*. Apparently the character of this variability is conditioned by the greater or lesser constancy of the supply of food.

Therefore, the fertility of arctic foxes is lowered according to the number of infertile and unmated females as well as to the death of offspring—the resorption of litters during the time of embryonic development and the death of pups after birth. In fox farms, unmated female averaged 7% at the end of the 1930's and those which were infertile—15%. Embryonic mortality attained 36%.

The sex ratio in populations of the arctic fox is almost 1 : 1, but this ratio may change depending on season, food conditions of the year and the age composition of the population. In the majority of cases observed, males predominate. In Kola and Saltykov fur sovkhozes [state farms], 2–3% fewer females were born. In the latter, during the period 1950–1957, deviations established a predominance of males in one year in one sector of the sovkhoz up to 4.4% (of 1100 pups) and the dependence of sex [in litters] on the age of females; in the litters of young (up to 2 years) and the old (6–8 years) females, males predominated (51–54%), while in those of moderate-age—females (51–51.5%). An increased number of males was observed in large litters (Ivanter, 1962).

On Yamal, at the beginning of the 1930's, 50.5% males were caught in one party, but here in 1933/34, females predominated (51.6%). In Bol'shezemel'sk tundra, at the beginning of the winter of 1956/57, the take of males was 56.4%, but by the middle of winter, there was no difference. On the Taimyr peninsula, at the beginning of the winter of 1931/32, 64% females were caught. Among 2182 arctic foxes obtained on the Commander islands, males constituted 53.8%.

Under natural conditions arctic foxes are usually monogamous, but individual cases of polygamy are known, it being observed on the Commander islands each year. This capacity of arctic foxes is used in breeding the animals on farms where only one male is kept with 4–5 females; individual males can accomplish 20–25 matings. Cases of polyandry, observed on the Commander islands, are extremely rare.

The ratio of young to adult animals in arctic fox populations changes considerably depending on feeding conditions, time of year, and on their total number. On the Lena, 62.9% young were caught

*Not in Literature Cited.; probably Lack, 1954, p. 46—Sci. Ed.

in the good year of 1935/36. In the Kara region in the season of 1956/57, a quite abundant one, during the time of peak migration more than 2/3 of the females were young⁵⁵; in the second half of winter, the latter constituted only 1/3 of the animals taken. In Yamal, the prevailing majority of individuals in the populations (in three harvest seasons from 1955/56 to 1957/58 inclusive; 475 individuals—94.7%), were determined as juveniles*. The ratio of adults to young animals constituted 1 : 18.9; this explains the selection of harvesters in direct ratio to the young animals (Smirnov, 1959, 1959a). Such abundance of young animals over a duration of 3 years otherwise seems improbable.

Arctic foxes reproduce well for 1–2 years in succession, after which they “rest” for 1–2 years. This periodicity observed repeatedly in the 1930’s in the Kola fox sovkhos was explained by “physiological exhaustion” of the female organism in which the first symptoms of overwork were revealed in the third year after the first two; the older the female, the lower the probability of its participation in reproduction at this age. Arctic foxes of late litters (in captivity) do not always reproduce the next year.

By means of the artificial insemination of silver-black foxes with arctic fox sperm, the mating of female red fox with blue arctic fox, and blue arctic fox female with the silver-black and white-muzzled foxes, hybrids of arctic fox and red fox were obtained. 243 These hybrids had the intermediate characteristics of both species but all of them were shown to be sterile.

Growth, development, and molt. White arctic foxes are born covered with dark smoky-brown short fur, while blue arctic foxes—with dark-brown, almost chestnut. As in young red foxes, newborn arctic foxes are born blind, without teeth, and with ear pinnae closed. They are smaller than [newborn] red foxes and weigh from 60 to 85 g; their body length is 11–13 cm; tail, 4.2–6 cm. Soles of paws are bare, but already by the fourth day they begin to develop fur.

Growth in the animals proceeds more intensively than in young red foxes. Eyes open on the 9th–18th day, simultaneously with the opening of the external auditory meatus. Eye color darkens over time. In the blue arctic fox, the eyes are bluish-gray at an early

⁵⁵Uterine determination of age (Chirkova et al., 1959).

*The Russian word *sevoletki* literally means “this summer’s”—Sci. Ed.

age; they turn yellow in approximately the 7th month. On the 12th day, the irruption of the incisors can be noted, and in some pups, the carnassial teeth also. On the 15th day all the incisors on both jaws have irrupted. Canines appear first in the lower, and then in the upper jaw. On the 18th day, the premolars are cut, first in the lower jaw. All milk teeth have appeared by the 27–28th day. Replacement of [deciduous] teeth by the permanent ones takes place in wild arctic foxes in the end of summer and the beginning of autumn in the cross and blue fox types (see below) (Zhitkov, 1913; Kozlova, 1933).

In one-year-old animals on Yamal in winter, the teeth are snow white and bright without any sign of wear. In contrast to the red fox, tooth wear with age begins with the upper incisors, proceeding to the first and second molars of the lower jaw. Earlier than in red fox, the fourth upper premolar is worn down and, later than in this species [red fox], the first and second molars of the lower jaw [are worn down]. Age determination by tooth wear was shown to be possible by also taking into consideration the changes in the proportions and configuration of the skull (Grigor'ev and Popov, 1952). Age determination according to the degree of closure of the central canine cavity is also possible. In this case, only the first two years age groups can be clearly differentiated (Smirnov, 1959, 1959a).

With age, the skull undergoes changes. In the young continental arctic foxes still with milk teeth, the posterior region of the skull is higher, and the nasal region is shorter and wider than in adults. Orbits smaller. Zygomatic arches thinner and narrower, bullae osseae more swollen and rounded, hard palate wider, sagittal crest absent or weakly developed. Later, the skull broadens in the area of zygoma and frontal region, which is abruptly elevated. The postorbital processes are large and the postorbital constriction is well defined. Muzzle elongates, sagittal crest is greatly enlarged, especially noticeable in Commander arctic foxes (Ognev, 1926).

At the age of 5–7 years, all teeth in Commander arctic foxes are worn down. Duration of life of arctic foxes assigned to island husbandry and sovkhoses for breeding service is 6–10 years. A case is known of an arctic fox living in a zoo for 20 years, when the animal died in a state of complete senility (Paramonov, 1929; Boitsov, 1937; Il'ina, 1949–50). Under commercial conditions, arctic foxes very rarely survive to old age. In the forest-tundra on the Yenisei, a very old arctic fox was caught in which only the crooked

remains of completely obliterated teeth were left; the pelage was short—about 2 cm in height, tail thin, but the animal itself looked very large (A.F. Chirkova). On Yamal, in the winter of 1958/59, when the number of young was small, only 5.5% of the arctic foxes caught were older than 3 years of age (Smirnov, 1960).

Arctic foxes grow quickly, especially at first. Thus, the average daily weight gain on farms decreases from 13% of body weight in the first days to 2.5% at the age of 2 months. Increase in weight depends also on food composition. On Kil'din Island husbandry on a mixed ration gave a daily weight increase of 20–40 g from days 244 42 to 90, an average of 28 g; those kept on fish ration, gave an average daily weight increase of 41 g and those on seal meat—54 g. Increase in length changed also. In farms, the average weight of pups at the age of one month was equal to 600–650 g, at two months—1.7–1.8 kg, at three—2.5 kg, at four—3.8 kg, at five—4.5 kg and at six months—5 kg. At 6–7 months, the young arctic foxes have almost attained adult size. From the age of 7 months to 2.5 years the weight of arctic foxes on farms increases on average from 5.6 to 7.1 kg in males, and from 4.9 to 6.2 kg in females.

The change in the weight of the pups of the early and late litters is greatly different: on a Kola fox sovkhov, this difference reached 1.5 kg at the age of 4 months. As compared to the red fox, the growth constant of the arctic fox before sexual maturity is larger, and in the sexually mature animals, smaller. Growth of the arctic fox is more quickly completed than in red foxes (Boitsov, 1937; Tavrovskii, 1946; Il'ina, 1952).

In nature, young arctic foxes had the following dimensions: on Yamal, July 2, weight 1250 g, with body length 40 cm and tail 16 cm; August 24 on the Khatanga, body length 51 cm and tail 21 cm; in October, on the Kolyma, a young blue fox (see below) weighed 3 kg with body length 54 cm and tail 32 cm; the latter animal had already attained adult dimensions (Zhnikov, 1913; Tsetsevinskii, 1940; A.F. Chirkova).

Seasonal variations are well manifested. Body weight of arctic foxes is lowest in summer and highest in December. In connection with rut and mating, weight drops greatly in the second half of winter, especially in males. On the Commander islands, it decreased by 15–20% as compared to that in December–January (Boitsov, 1937; Il'ina, 1940, 1950).

In the white arctic fox, the following age and seasonal stages of the pelage are differentiated (Paromonov, 1929; Boitsov, 1937; Guber, 1939; Rakhmanin, 1948; N.N. Spitsyn). *Slepushonka** [mole-vole] or *kopanets** [digger] has a delicate dark-brown, almost black fur, with very sparse, separately protruding guard hairs. Skin length 30–35 cm (without tail); age up to 1–2 months. In the *nornik** [burrow dweller], the quantity of guard hairs is somewhat greater and the pelage turns browner; the back, shoulders, head and tail darken. Skin length without tail 40–45 cm. It still lives in the burrow; age 2–4 months. *Krestovatik** [cross fox]—the arctic fox in summer coat, distinguished by brightening of the pelage on the belly and along the sides, acquiring a grayish straw-colored tone. The brown stripe along the back and on the shoulders is clearly marked, in the form of a cross, and guard hairs are considerably better developed than in the preceding stages. Skin length of the young cross fox 45–60 cm, of tail—30 cm. *Sinyak** or *chayachnik** [blue fox] has a shorter pelage; following upon the appearance of a large amount of white hairs, it becomes lighter and grayer, taking on a bluish, leaden tone. Skin length without tail—54–68 cm, tail length—32 cm. Guard hairs up to 40 mm in length. Age, 6–8 months. Arctic foxes are found in this stage from the end of September to the middle of October. Replacement of the milk teeth by the permanent ones takes place in the *krestovatik* and *sinyak* stages. In the *nedopesok** [premature], fur is grayish-white, with scattered brown guard hairs concentrated on the upper part of the body. Underfur azure-blue. The animal is found in this pelage from the middle to the end of October. Complete, full-grown or *doshlyi** [finished]—this is the arctic fox in its winter white fur; some animals only retain a few “bead” guard hairs, and light bluish color at the base of the hairs. Wool is dense and fluffy. A few arctic foxes attain the full winter pelage by the end of November, but the majority in December–January.

In full winter pelage, the so-called standard arctic fox is divided into 3 sorts depending upon the degree of maturity, whiteness, length and evenness of guard hair distribution, and the thickness of the entire pelage. Not all arctic foxes reach full fur development each year. The greater part of the skins prepared during the course

*Translator's remark: These local names (on this and the following pages) are transliterated, and the literal English meanings given in brackets.

of a winter are of the second and third sorts. In first year arctic foxes, full development of fur cover is rarely attained. The most high quality furs are supplied by 3–4 summer [2–3-year-old] males and 2–3 summer [1–2-year-old] females. Emaciated arctic foxes, and individuals, often frequenting burrows, or living within thickets of stunted *tal'nik* [purple osier] are distinguished by dull and frayed fur.

At the end of winter, when the still white and fluffy fur of the arctic fox begins to weaken and “leak”, the animal enters the *veshnyak* [spring] stage. Later, usually in April, during the formation of the summer hairs and the darkening of the flesh side of the skin, the almost guard-hair-less skin is called “*gagara*” [loon]. After shedding of the winter hairs, the adult arctic fox again enters the summer stage—*krestovatik*, which differs from the young animal by its firmer pelage; length of guard hairs is about 1.5 cm. This completes the cycle of seasonal pelage change. Throughout the course of their lives, the adult white arctic foxes annually go through these described stages of pelage replacement, except for *slepushonka* and *nornik*.

The pelage of the blue arctic fox changes with age and to a lesser extent, with the seasons. From the almost black or dark brown (*slepushonka*), the fur of the adult arctic fox gradually lightens, and acquires a dark violet to light-beige color. With age, it is mainly the tone of the hair color that changes. At the end of August on the Commander islands, the majority of arctic foxes already have a normal “blue” colored winter pelage. Some fur categories are differentiated—gray or brown tones on Bering Island and chocolate on Mednyi Island. Hair softness also varies. Arctic fox fur becomes completely “*vykhodnyi*” [grown out] in the second half of December–January. Average length of contour hairs in the 1.5–2-month-old arctic foxes is about 27 mm, on winter skins, more than 82 mm; in winter, hair thickness also increases. As a result of the warm and humid climate on the Commander islands and especially in connection with the delayed arrival of cold, the fur of those arctic foxes is distinguished by coarser and shorter guard hairs and often by matted underfur (Tret'yakov, 1871; Barabash-Nikiforov, 1937; Boitsov, 1937; Il'ina, 1949, 1950).

In adult arctic foxes molt takes place twice a year, in spring and autumn. On farms, arctic foxes have a full winter fur cover from December to February. Spring molt proceeds from the end of



Fig. 90. Blue fox in summer fur. Mednyi Island. Photograph by N.N. Kartashev.

February to June. Summer hairs are initiated in April and grow until the middle of August. Autumn molt occurs in August–September, while the growth and maturation of the winter pelage takes place in October–December. Guard hairs in winter are twice as long as in summer (an average of 45.8 mm, and underfur 37.9 mm), and the hair thickness is also greater. Underfur quantity constitutes 97% (Eremeeva, 1956; Kaletina, 1956; Kaletina et al., 1957). In winter there occurs an abundant deposit of subcutaneous fat. Sweat glands at this time are weakly developed. In summer, the fat layer is reduced and the size of the sweat glands increases.

The beginning of spring molt coincides with the start of estrus. In the first instance, pregnant females molt, their skins losing winter fur just after parturition. Males, barren females and yearlings molt later, and the last are old and diseased animals (A. Romanov, 1941 and others). Holding arctic foxes at higher temperatures ($18 \pm 20^{\circ}\text{C}$) and lower humidity ($42 \pm 8\%$) speeded up the time of spring molt by 8 weeks (Il'ina, 1926).

In the wild, the time of pelage replacement of arctic foxes varies greatly depending upon meteorological conditions, the abundance of food and nutritional state of the animals, their age, sex and the physiological condition of different individuals. Spring molt begins earlier and occurs more rapidly in years with good food conditions. In the southern tundra zone, spring molt begins 1.5–2 weeks earlier and ends 2–3 weeks earlier compared to the northern coast and the Arctic Ocean islands (Rakhmanin, 1959). Molt of arctic foxes in February was observed in different years on the Kola peninsula, Yamal and even on Belyi Island. More often, the onset of molt is observed in March, and on Taimyr and Novaya Zemlya, even in April. In various populations, it extends for 4 or more months and in the first 2 months is usually not obvious. Shedding of winter fur ends in the majority of tundras in June or July, but significant individual deviations are observed. On Klimets Island (Lake Onega) in the middle of June, a half-white arctic fox was killed (Sluchevskii, 1886). Individual unmolted arctic foxes are encountered even in August. On Novaya Zemlya in the beginning of May and on Yamal at the end of May, some individuals were found in winter pelage, and on the New Siberian islands, arctic foxes were white even at the beginning of July (Krivosheya, 1884; Paramonov, 1929; Dubrovskii, 1937, 1940; Tyulin, 1938; A. Romanov, 1941; Rakhmanin, 1959). In Greenland (Seton-Thompson, 1909–1925), arctic foxes are met with which, as in hares, are not able to change the winter pelage during the short summer and remain white throughout the year.

Spring molt starts with the shedding of the guard hairs, then underfur which is, however, more quickly replaced than guard hairs. Replacement proceeds from the end of the muzzle, rump and tail base, spreading along the back in the shoulder region, on the limbs and later—on the side and belly. Winter hairs are retained longer on the tail. During the formation of the summer hair cover, darkening of the flesh side of the skin begins around the eyes, at the base of the tail, on the rump, forefeet and then spreads to the thighs and back.

Autumn replacement of hair cover proceeds in the wild from September to December. Better fur occurs in January–February. Time of autumn molt is delayed in the south for 2–3 weeks in comparison to northern regions (Rakhmanin, 1948, 1959). Thus, earlier maturation of fur was observed on Belyi Island (about 73° N. Lat.), where at the end of September 1930, arctic foxes

wandering over the snowless land were sharply distinguished by their already whitened skins. On the eastern coast of Severnyi Island of Novaya Zemlya (Sedova gulf, 75° N. Lat., Ledyanaya Gavan'), during observations on 12 September and October 1936, arctic foxes in white coats were also encountered (Rundan, 1936; A.F. Chirkova). Fur maturation proceeds asynchronously in arctic foxes of various [fur] types. In Kara region, in December 1956, among arctic foxes of the Pechora type caught, 33.5% of the skins were of sort 1 [see above], and among arctic foxes of Obdorsk type, coming from the higher latitude of Yamal—79.7% (Chirkova et al., 1959). On the Commander islands, maturation of fur at different times by habitats ("ukhozh")* is well known; animals from rivers in montane barrens have better coats. From the second quarter of this century, when the climate of the islands warmed noticeably, autumn pelage appeared later. Earlier, harvest began here in November–December, when the fur of the majority of arctic foxes was already mature; at the present time, for gathering better skins, arctic foxes are killed at the end of January and in February (Il'ina, 1949–1950).

Falling temperature and increased humidity, especially in October, have a favorable effect. Humidity influences increase in guard hair length and fluffiness. Nutritional status, sex, age, and physiological condition of the individuals affect the time of autumn molt. It was noted that the more abundant the food in autumn and beginning of winter (but not in summer), the longer the delay in maturation of fur. Fur matures earlier in males, and later in barren females. The young of late litters develop full coat later than adults. Molt of old and diseased individuals is delayed.

Full pelage growth takes place at different times in different years. On Yamal in the winters of 1923/24 and 1924/25, when the numbers of arctic fox was low, *sinyak* [see above] constituted 1.2–2.0%, i.e., winter fur of arctic foxes developed comparatively early, but in 1925/26, when arctic foxes were abundant, this group constituted 20%, *nedopesok* constituted 18%, and top quality fur was only 30%; i.e., growth of winter fur was greatly delayed. In the winter of 1927/28, when arctic foxes were few, *nedopesok* constituted 8%, and top quality furs were 45% (N.N. Spitsyn); i.e., growth of winter fur proceeded more intensely. In the lower Lena,

*See previous footnote, p. 346—Sci. Ed.

in the winter of 1935/36, when arctic foxes abounded, *sinyak* were encountered throughout the winter (in February 0.4%). Skins of sort 1 in the March collections were 23.2%—development took place slowly (Tavrovskii, 1939). In the Taimyr National Region in the winter of 1945/46, in all, 5.3% sort 1 skins were processed while in the winter of 1936/37—30.6% (N.N. Kuznetsov). On Novaya Zemlya, individual arctic foxes with dark ears and tail tips are sometimes seen throughout the winter. Arctic foxes with incompletely developed winter fur in any case begin spring molt also in February and March (Tsetsevinskii, 1940). Therefore, in years of comparatively good food conditions for the young, in years of a low number of animals, the development of the winter coat is accelerated, while in the absence of food in years of intensive reproduction of arctic foxes, it is delayed.

For Lena-Khatanga territory the following scheme was proposed for seasonal changes in hair cover of the arctic fox (A. Romanov, 1941)⁵⁶.

January–February—all arctic foxes “*doshlyi*” [finished], skins sorts I, II and III.

March—predominance of first sort skins; in second half of month, rarely *veshnyak* [spring] (the first molt stage).

April—“*veshnyak*” predominates; in second half of month “*gagara*” [loon] appears (beginning of intensive molt).

May—“*gagara*” predominates (intensive molt).

June—all arctic foxes in “*gagara*” stage (end of molt).

July—all arctic foxes transit to *krestovatik* [cross] stage.

August—all arctic foxes in *krestovatik* stage.

September—*krestovatik* predominates, a few *sinyak* [blue], rarely, *nedopesok* [premature].

October—*krestovatik*, *sinyak*, *nedopesok*; rarely “*vykhodnyi*” [grown out].

November—*sinyak*, *nedopesok*; *vykhodnyi* predominates with skins of lower sorts [II, III]; a few first quality.

December—*vykhodnyi* skins of all sorts, sort II predominates; *nedopesok* is rare.

⁵⁶Other evidence of A. Romanov was also taken into consideration on the development of arctic fox fur in the winters of 1925/26, 1926/27 and 1934/35, with different environmental conditions.

The topography of hair cover replacement in autumn differs from that in spring. Molt also begins with the head, which turns gray on the sides, but subsequently, whitening takes place on the groin and on the sides of the body, and later on the back and tail. On the back, individual dark hairs are retained for a long time. Sometimes, whole areas of the fur on the nape remain unmolted. During the time of the autumn molt the flesh side of the skin in white arctic foxes remains light, but in the blue, it darkens; at first, the flesh side grows thick, but later becomes thin.

Among the pelage variants of white arctic foxes, cases of partial chromism in the form of sharply delimited spots of foxy color are noted. In the Bol'shezemel'sk tundra, white arctic foxes were caught with spots of reddish fur on the side or on the posterior part of the back, from 2–3 to 10–15 cm and larger. Spotted individuals were observed in the years with an abundance of arctic foxes. In January 1947, in Nizhnii Kolymsk region, an arctic fox was caught with a bright-reddish spot 6.3×19 cm in diameter.

Enemies, diseases, parasites, mortality, and competitors. Enemies of the arctic fox are few. Among them are the wolverine and wolf, which are found in tundra in some numbers. The polar bear rarely attacks the arctic fox, but in the years of famine, it may harass the fox to death. The main enemies are sled and herders' dogs. Among birds, the golden and white-tailed eagles, the large species of gulls (glaucous and others) and skuas, raven and even crow are dangerous (to young), and on the Solovets islands, also goshawk. More often, the white polar [snowy] owl annoys the arctic fox, being especially numerous in the years of intensive reproduction of the animal; in the taiga zone—eagle owls. Owls attack young arctic foxes during their dispersal from burrows and also kill those weakened by disease or migration. Owls are periodically very abundant in the tundra. Thus, in Bol'shezemel'sk tundra 600 birds were trapped in spring, summer and autumn 1955 in an area of about 400 km² (Yu.V. Rybalkin).

In years of insufficient food with an abundance of animals and intensive migration, epizootics are common in the migrants (Chirkova, 1951, 1955; Sokolov and Cha, 1957; Meteleva and Rubanchik, 1959; Chirkova et al., 1959). Native inhabitants have long been acquainted with the disease called here *dikovan*', or frenzy [rabies], "plague".

Losing their sense of fear, furious arctic foxes run into villages, enter dwellings, attack dogs, reindeer and humans. Animals bitten

by arctic foxes become rabid, but the disease is extremely rare among people. Scars and gashes on the muzzle and other body parts of the arctic fox indicate that the animals often bite each other, and this influences the rapid spread of the disease. Usually many other species are involved in a rabies epizootic: red foxes, wolves, wolverines, ermines, weasels, sled and hunting dogs, hoofed animals and even birds—owls, gulls and others which feed on lemmings. The disease among arctic foxes is usually preceded by the massive death of lemmings.

The bodies of dead arctic foxes are not often observed in the winter period, and only after the disappearance of snow is the size of the epizootic revealed. Thus, in the spring of 1933, in the middle of Yamal, the remains of 16 arctic foxes which had died in autumn and winter were found along an extent of 20 km². In the same year, in the Se-Yaga region, 130 dead bodies of arctic foxes were discovered in an area of 3000 km²; the majority were in winter fur and high nutritional status. In the Pechoro-Ilychsk preserve, in the second half of winter after the massive migrations of arctic foxes in 1929/30 and 1935/36, disease was observed with the death by spring of nearly all immigrants. In the next season, disease was observed among dogs similar to that of arctic foxes and much mortality among them (Teplov, 1960; A.F. Chirkova).

Large epizootics among arctic foxes took place, from the end of 1946 and in 1947 in almost all expanses of tundra in the USSR after the disappearance of lemmings (following unfavorable meteorological conditions in 1946 and 1947). By the spring of 1948, surviving arctic foxes were scarce everywhere, reproduction proceeded slowly, and their numbers sharply decreased by the season of 1948/49 in all tundras of the Soviet Union, except for the Far East where their reduction in number had occurred in 1947 (Chirkova, 1955).

At the beginning of the winter of 1953/54, in northern Yakutiya, soon after an outbreak of lemmings, disease appeared among arctic
 249 foxes. The diseased or dead constituted about 15% of those obtained, and all were well nourished—the arctic fox fed on the dead lemmings. The disease followed a swift course, and was transmitted to dogs, wolves and reindeer. Later, starvation of arctic foxes, migration and sharp suppression of reproduction were observed in 1954; about 1/3 of the females were left unmated and more than half of them remained barren (Tavrovskii, 1958). Only among

arctic foxes of the Commander islands were epizootics not observed. The number of animals is always sharply lowered as a result of epizootics, and the intensity of reproduction of the surviving animals sharply decreases.

The study of rabies—a neuroviral disease of arctic foxes—was promoted in the extreme northeast of Bol'shezemel'sk tundra from 1954 to 1962 (Kantorovich, 1956, 1957, 1963). It was established that outbreaks of the epizootic among arctic foxes took place in 1947/48, 1951/52, 1954/55 and 1955/56, with moderate disease incidence (up to 10 cases) in 1949/50, 1952/53, and 1958/59 and 1961/62, with simultaneous cases among dogs and individual occurrences among wolves, red foxes and reindeer. The disease was observed exclusively in the cold months of the year from November to March. Examination of the brains of 1596 healthy arctic foxes over the course of 6 summers revealed that in general 30% were carriers; in years of massive outbreaks or moderate incidence—30–75%, and in the absence of the disease—3–6%. The virus was also isolated from red foxes. In healthy wolves, ermine, mouse-like rodents (Siberian lemmings, voles), owls and dogs, the virus was not detected, and therefore the arctic foxes were considered the permanent carriers of rabies infection in the far north. The virus was isolated from young arctic foxes, and from males twice as often as from adults, or from females. The virus was also isolated in the parotid and submaxillary glands in the years of outbreaks in 20–30% of cases, but outside the disease period, in low numbers of arctic foxes, and in the absence of migration—only in individual cases.

Rabies in arctic foxes was also studied in the tundras of the Nizhne-Kolymsk region during the epizootic of 1958/59. It was shown that in intramuscular infection of 6 arctic foxes from arctic foxes, red foxes and dogs spontaneously ill with rabies, the incubation period ranged from 10 to 18 days, after which all arctic foxes became sick and died within 2–3 days. At that time hydrophobia disappeared. All animals died in a condition of outstanding good nutrition. Pathological changes in the diseased animals were revealed only in the form of hyperemia in the brain. Babesh-Negri bodies were not detected in the diseased arctic foxes examined. The retention of the active virus in the frozen brain was confirmed after 202 days. Not a single case of disease among people was established, even after being bitten by rabid animals. However, the

question of virus pathogenicity to humans through various routes and dosages was not studied (Strogov, 1961). The disease is characterized as a viral arctic encephalitis of animals (Stroganov, 1964).

Under natural conditions, the arctic fox is susceptible to leptospirosis (infectious *zheltukha*), especially at a young age, but in a mild form. The role of agent of leptospirosis in arctic foxes, red foxes and other animals is served by *Leptospira icteroanaemiae*, and in addition, this disease in both species is induced by *L. icterohaemorrhagiae* (causative agent of Vasil'ev-Wel's disease in humans). Animals and humans are both susceptible to leptospirosis (Vyshel'skii, 1954).

Outbreaks of epizootics among arctic foxes was observed in Bol'shezemel'sk tundra in 1909/10, 1926/27, 1929, 1932/33, 1937/38, 1943, 1947/48, 1955/56 and 1957/58; on Novaya Zemlya, in 1891, and also in 1927 and 1932/33; on Yamal in 1923, 1928, 1930, 1932/33, 1934/35, 1935/36, 1947/48, and 1957/58; in northern Krasnoyarsk territory in 1915/16, 1920, 1923/24, 1926/27, 1935/36 and 1947/48; in Lena-Khatanga territory in 1926/27; in northern Yakutiya in 1944, 1946/47, 1950/51, 1953/54 (from the Yana to the Kolyma) and in 1947/48 (Olenek-Lena); on the Anadyr in the beginning of the 1880's, in 1890, 1903/04, and on the coast in 1944/45.

250 On fur farms and nurseries [*sic*], arctic foxes suffer from paratyphoid which carries off to 50% of the young, especially of the late litters; this disease has been known in the USSR since 1933 and is caused by the bacterium *Salmonella cholerae suis* and *S. typhi murium*. There are references to the presence of canine distemper, Aujeszky's disease, pneumonia and tuberculosis and rarely anthrax among arctic foxes. In years of outbreaks of the latter among reindeer, much mortality was also observed among arctic foxes (Lyubashenko, 1941; Vyshel'skii, 1954; Sludskii, 1954; Lyubashenko et al., 1957; Pankov et al., 1957; N.N. Spitsyn).

Skin diseases of arctic foxes in the wild have not been studied. In years of this epizootic disease, arctic foxes appear with incompletely developed coats, with bald patches and other damage (Rutilevskii, 1939; Rakhmanin, 1948; Chirkova, 1955 and others). In the European north, in 1945/46 and 1946/47, bald patches and "stunted" pelage were observed in arctic foxes. At the mouth of the Pechora, in February, 1956, at a time of epizootic, an arctic fox with scabs and almost bald was caught. In tundras of the Far East,

in 1944/45, among a great number of sick arctic foxes, up to 70% "spoiled" coats were encountered.

In two arctic foxes from Yamal in 1957 and 1959, 5 species of external parasites were found: the gamazid mites *Laelaps lemmi* and *Hirsutionyssus isabellinus*, the fleas *Ceratophyllus penicilliger* and *Leptopsylla ostsibirica* and the biting louse of the snowy owl, *Strigiphyllus ceblebrachys* (Luzhkov, 1963).

In arctic foxes of the Commander islands, scabies was observed in some cases, caused by *Sarcoptes scabiei* (0.4%). On Bering Island, the mange mite (*Demodex canis*) was observed—a serious, usually chronic skin disease (7% animals infected), which was widespread among arctic foxes in the 80's of the past century and which was, probably, transmitted from dogs. On the Commander islands, the ear tick *Otodectes cynotis* and the biting louse *Trichodectes canis* were found on arctic foxes; sucking lice were observed [pediculosis] (1.6%) and they were struck with ringworm [trichophytosis] and moist ringworm (0.7%) infections. In 1935/36, of 61 arctic foxes examined, 27 were observed with these diseases and in 34 arctic foxes the biting louse and sucking louse were found.

Infection with endoparasites among arctic foxes is almost 100% (Isaichikov, 1931; Dubrovskii, 1937, 1940; Kirpichnikov, 1937; Kolmakov, 1937; L. Popov, 1939; Rutilevskii, 1939; Shastin, 1939; Afanas'ev 1941; Petrov, 1941, 1958; A. Romanov, 1941; Pereleshin, 1943; Il'ina, 1949, 1950; Dubnitskii, 1953, 1957; Chirkova et al., 1958, 1959; Britov, 1959; Petrov and Kosupko, 1959; Ovsyukova, 1961; Luzhkov, 1963). In the USSR, more than 30⁵⁷ helminth species were found in arctic foxes, of *Nematoda* (11 species), *Cestoda* (10 species) and *Trematoda* (7 species) and two species of *Acanthocephala* (found in arctic foxes on fur farms).

The nematode *Toxascaris leonina* is found in the intestine and stomach of arctic foxes nearly everywhere, and in the majority of animals; of 59 arctic foxes from the neighborhood of Kara, 84.8% were infected, on Yamal, of 118 animals in a year of depressed numbers of arctic foxes—92.4%. On the Commander islands, the fluke *Maritrema* sp. (80–100% infection) and the cestode *Mesocostoides lineatus* (88% on Bering Island) are found; each

⁵⁷There are 55 species of parasites known; one species of Protozoa, 44 species of parasitic worms and 10 species of external parasites (Luzhkov, 1963).

individual contained some thousands of both species. The nematode *Uncinaria stenocephala* is very often met with, and infects young animals more intensively. The nematodes *Spirocerca lupi* and *S. arctica* invade the stomach (goose egg-size tumors); the latter induce extreme emaciation and susceptibility to rabies. Trichinosis is known in 34% of some populations.

251 A great danger presented by arctic foxes is their infection with the cestode *Alveococcus multilocularis*, found in the adult stage in the intestine of 50.8% (among 59) of arctic foxes in the winter of 1956/57 in the northeastern Bol'shezemel'sk tundra; in some animals up to 200 thousand specimens were found. On Yamal, the infection rate in 1957–1959 reached 73.7% (in 118 arctic foxes, from 11 to 74 thousand specimens were found in each animal). In the Anadyr and Iul'tin tundras (Chukotka), the total infection was 62% (among 35 arctic foxes) with intensive invasion by hundreds and thousands of specimens (Ovsyukova, 1961). Apparently, it is this form of echinococcus that is found in arctic foxes on Kil'din Island, the Commander islands, and in continental arctic foxes of Yakutiya. This parasite, when present as large infection in arctic foxes, induces extreme emaciation and paralysis. On Yamal, arctic foxes are also heavily infected with the tapeworm *Taenia polyacantha* (in 86.4% of animals) and *T. crassiceps* (in 46.6%). *Trichinella spiralis*, which induces a rise of temperature and paralysis of respiration resulting in death or chronic illness, was found in arctic foxes of the Commander islands and in some other regions of the Far East (Petrov, 1941).

Species of massive infection—echinococcus and the majority of taeniae—are transmitted through small rodents. The burrows of arctic foxes are the foci of toxascaridosis. Echinococcus as well as the trematodes *Opisthorchis felineus* and *Metagonimus yokogawai*, the cestodes *Diphyllbothrium latum*, *D. erinacei* and *D. caninum*, and the nematodes *Trichinella spiralis* and *Toxascaris leonina* are pathogenic to humans also.

The majority of helminth species of arctic foxes are found in the gastrointestinal tract, mainly in the small intestine (in 100% on Yamal); one trematode species—in the bile ducts of the liver, 1 nematode—in the urinary bladder, 2 nematodes—in the bronchi, trachea and nasal cavity, and 1 nematode—in the stomach. The larval stage of one species of cestode lives in subcutaneous cellular tissue, and one trichinellan—in the muscles. Coccidians were found in

the liver and intestinal tract of the arctic fox. Each arctic fox (Bol'shezemel'sk tundra, Yamal) is infected by up to 4 species of endoparasites. The degree of parasitic infection on the Commander islands is related to the nutritional condition of the animals (Afanas'ev, 1941). In almost all arctic foxes, enteritis is noted as a result of the effect of helminths; in the presence of heavy infection with alveococci, there is subacute necrotic enteritis. Helminthiasis reduces fertility and induces the death of animals. Helminths of arctic foxes are shared in common with red foxes, wolves (4 species on Yamal) and dogs. Infections of arctic foxes in the northern regions are less than in the south (L. Popov, 1939; Rutilevskii, 1939; Chirkova et al., 1959).

Death of arctic foxes due to basic hardship frequently takes place in the cold period of the year. During ice-glazed periods, the arctic fox's claws become broken and it cannot obtain food in the littoral zone and the tundra. Arctic foxes caught on the thin autumn ice of the open sea often perish in great numbers. Along the western coast of Yamal and in Baidaratsk bay, dead arctic foxes are collected in tens or hundred in some years. Many animals die at the time of seasonal migrations in the unusual situations of the forest zone and Arctic seas, whence they come in hundreds in autumn, and in spring return individually. Arctic foxes often drown crossing large rivers, for example, the lower Pechora with its numerous branches. On the Nizhnii Taimyr, of 46 arctic foxes swimming across, an observer saw three drift out to sea and three die in the river.

Several facts attest to the great vitality of arctic foxes. On the lower Lena, an arctic fox was noticed with a badly broken paw; gangrene had already appeared, and it weighed only 1075 g. On the Commander islands, a blind female with cataracts in both eyes, stumbling against rocks while running, brought into the light a litter and nourished them.

On the Commander islands, arctic foxes died from eating salt fish. Dead animals were found with pathological changes in the
 252 kidney and with ulceration of the stomach and intestine; cases of pneumonia and emphysema were noted. Sometimes inexperienced mothers bite, and tear at, or drag about their young. Deficiency of milk may incite such mothers. Newborn young die mainly in the first days after parturition. Mortality among pups up to 10 days old constituted 22–24%, from 10 to 30 days old—3%, from 1 to 2 months—

8%; i.e. the total number of deaths among young at the end of lactation was 34% (of those born). From 2 to 5 months of age, 3% of the whelps died, and total mortality through the period of attainment of sexual maturity—about 40%. On the Commander islands mortality through yearling age of 33% was noted; on farms in Canada—33–46%. In the Commander island enterprises in the 1930's, mortality among arctic foxes in July–August around an “*ukhoz*” [foraging site] varied from 8 to 15%. Mortality among adults constituted about 5% per year.

On Mednyi Island, of arctic foxes that died in the period of 1930–1935, 20% died from injuries and fights, 13% from poisoning by salted products, about 37% from diseases and 30% from other causes. On Bering Island, 21% of the arctic foxes taken in 1937/38 were diseased.

Under natural conditions of the continental tundras, the magnitude of mortality, like that of reproduction, varies considerably in various years as a result of the great fluctuation, above all in the food supply. Judging by post-parturition placental scars in the uteri of arctic foxes in northeastern Bol'shezemel'sk tundra in the summer of 1956 (a year with decreased number of arctic foxes), an average of 3.1% embryos were resorbed per pregnant female; 50% of the young females had died by the beginning of harvest. On Yamal in the summer of 1933, with negligible numbers of lemmings, about 80% of the young died. Almost a two-fold reduction in the number of young at the burrows was noted by “*Sluzhboi Urozhaya* [Harvest Management]” from May to September in various tundra regions of the Far North. To control mortality of young arctic foxes in the wild, local *kolkhoz* [collectives] and *sovkhoz* [state farms] bring food to the burrows in food-deficient years in spring and summer, as well as in autumn in places of approach and harvest of the animals (Guber, 1939; Tsetsevinskii, 1940; G. Naumov, 1941; Skrobov, 1958; Chirkova et al., 1959).

During the past decade, a northward shift in the southern limit of reproduction has been observed. A series of authors (Rozanov et al., 1932; Skrobov, 1958, 1958a, 1960; Uspenski, 1963) consider this to be due to the colonization of red foxes in the forest-tundra zone, and to its deep penetration into the southern zone of tundra. However, the importance of the red fox as a competitor of the arctic fox is exaggerated, since the main food of the red fox is gray voles [*Microtus*] and of arctic fox—lemmings and marine flotsam.

Arctic foxes prefer to den in open, elevated parts of the tundra, while for the red fox it is river floodplains, mainly forested sections. The number of red foxes in the zone of contact of the ranges of both species is extremely small; in northern Arkhangel'sk district, in preparing skins during 28 years (until the season of 1962/63) for one red fox there were more than 10 arctic foxes and the difference between the number of both species increased in recent years. The process of displacement of the limits of reproduction of both species is governed, one may suppose, by changes in a series of abiotic and biotic factors as a result of Arctic warming; i.e., the effect of warmth on the soil and its moisture, on the microclimate of the burrow, on the duration of snow cover, on the time of the vegetative growth period, perhaps on the displacement of the limits of some plant and animal forms, in particular, the distribution of species of small rodents—lemmings, which are the main food of the arctic fox and gray voles, preferred by the red fox. Attacks on young arctic foxes by red foxes were observed, as well as of arctic on red foxes, in the course of ousting of one or the other species from burrows and places of activity (Rozanov et al., 1932; Boitsov, 1937; Dubrovskii, 1940; Skrobov, 1958, 1958a).

253 Direct competitors of the arctic fox for food are the ermine and weasel, but because of the small number of these species in the tundras, they do not inflict large losses on the arctic fox. In the lower Khatanga, where the arctic fox appears in great numbers there, the ermine disappears. In years of lemming abundance, they are also eaten by wolf, polar bear, wolverine, wild and domestic reindeer and even shrews, and thus they compete with the arctic fox. On Kil'din island, contests with river otters for fish were observed, and in the littoral zone of the Commander islands—with swines for marine flotsam. Sometimes, the wolverine uses burrows of the arctic fox. In its turn, in Yakutiya the arctic fox occupies the empty burrows of the tarbagan marmot and in the mounds of ground squirrels.

Everywhere in the tundra, the snowy owl competes with arctic fox for its main food which is also the small rodent; in years with many rodents, both the snowy owl and the arctic fox reproduce in great numbers in the tundra. The same was observed for the rough-legged hawk [*Buteo lagopus*], which is less numerous in the tundra. Small rodents are also eaten by 2–3 species of skuas [*Stercorarius*], peregrine, merlin, in some places short-eared owl, white-tailed eagle,

goshawk and, in addition, raven, crow, magpie and gulls; gulls and corvids feed together with the arctic fox in the littoral zone (Osmolovskaya, 1948).

Population dynamics. Seasonal dynamics in numbers of the arctic fox in years when its main food is plentiful is well manifested. Minimal population density is observed in spring, and the maximum at the end of summer—beginning of autumn, just after the litters abandon the burrows. When food is scarce, the growth of the population in summer is sometimes so negligible that the number of arctic foxes in autumn is even less than that in spring.

Annual variations in their numbers are extraordinarily sharp. Beginning in the middle of the last century, a 3-year repetition of “productive” years for the arctic fox was often noted, with fluctuations of from 2 to 6 years between years of abundance (Vrangel’, 1841; Brandt, 1856; Middendorf, 1869; Nosilov, 1909; Folitarek and Chirkova, 1930; Burke, 1936; Dubrovskii, 1937, 1939, 1940; Kirpichnikov, 1937; Guber, 1939; Rakhmanin, 1948; Chirkova, 1955; Sdobnikov, 1958 and others). During 35 years at the end of the past century and the beginning of the current one, the maximum supply of arctic fox skins at Irbit’sk fair was observed each 3–5 years, and at Yakutsk each 1–5 years (Silant’ev, 1898; Paramonov, 1929). During 1924–1959, maxima of prepared skins were repeated each 2–4 years⁵⁸. In separate regions of the north, after the October Revolution, the interval was 1–4 years (2–3 years on the average). During the last decade, some stabilizing of fluctuations is observed in the arctic fox catch. Apparently, this is a result of technical measures to improve hunting. The average catch of arctic foxes in this period increased (see p. 376). Fluctuations in the catch and in preparation of skins correspond, in general, to the dynamics in the number of the species revealed by the more or less accurate count of wild animals in nature.

There is great amplitude of variation in the numbers of arctic foxes in successive years. In the autumn of 1912, in the vicinity of Russkii Ust’ [Russian Mouth] of the Verkhoyansk region there was an extraordinary “raid” of arctic fox, “what mosquitos” as expressed by the natives (Zenzinov, 1914). Following such a year of

⁵⁸Not counting the war years, when in the USSR as a whole and in Krasnoyarsk territory, 5 years passed between 2 successive peaks, probably as a result of special economic conditions.

abundance, the arctic fox was rarely met with. The number of animals in census areas varies tenfold in various years. The number of breeding burrows changes from a small percentage in unfavorable years (Table 29) to full occupation of all breeding burrows and the appearance of pups even in temporary shelters in years of abundant reproduction of the species. In 1935, in the Kara region—in northeastern Bol'shezemel'sk tundra, in a year of growing numbers of the species, 39% of the burrows found were occupied by large litters and the total number of arctic foxes on the experimental plots increased more than 9 times as compared to the preceding year, when only 5% of the burrows were occupied and litters were fewer. In the same region in the winter of 1957/58, as compared to the preceding winter, the number of arctic foxes decreased 3.7 times (N. Dement'ev, 1955; Chirkova et al., 1959). On the northern shore of Taimyr Lake and along the Nizhnii Taimyr river, with intensive reproduction of arctic foxes in 1947, about 70% of the old burrows were occupied; in 1948, with weak reproduction, out of 18 old burrows examined, a litter was found in only one (Sdobnikov, 1958).

In the arctic tundra of the Nizhne-Kolymsk region in the summer of 1950, the greater part of the burrows were inhabited, and in autumn, the number of arctic foxes was high. In 1951, the number of arctic foxes sharply decreased and out of 205 burrows, only 11.5% of the burrows were inhabited; at the same time, in the southern zone of the tundra, where food is more varied, a concentration of arctic fox was noted. In summer of 1952, in the arctic tundra, out of 103 burrows 2.3% of them were inhabited, while in the southern zone—41.2% (of 34 burrows). In summer and autumn of 1953, with abundant lemmings in the arctic tundra, more than

Table 29. Occupation of burrows by arctic foxes in Turukhansk territory, around 69–70° N. Lat. (Boitsov, 1937)

Total burrows investigated	Of these, in %			
	With 3 pups	With signs		Uninhabited
		Permanent residence of adults	Rare visitation	
71	2.7	7.0	11.1	79.2

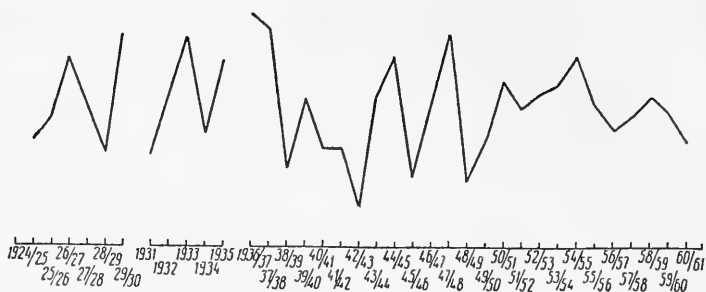
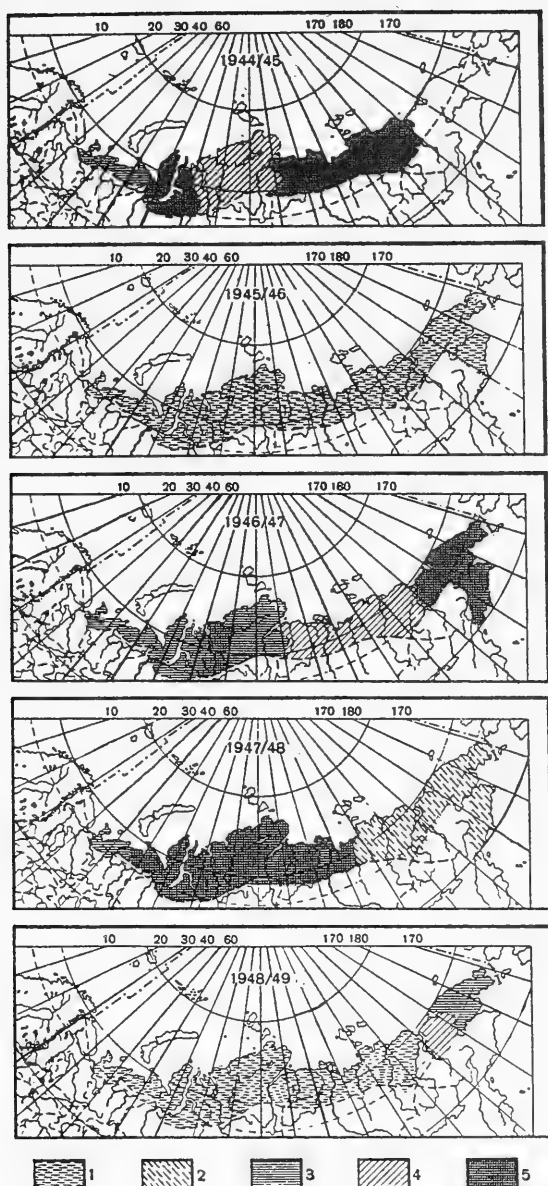


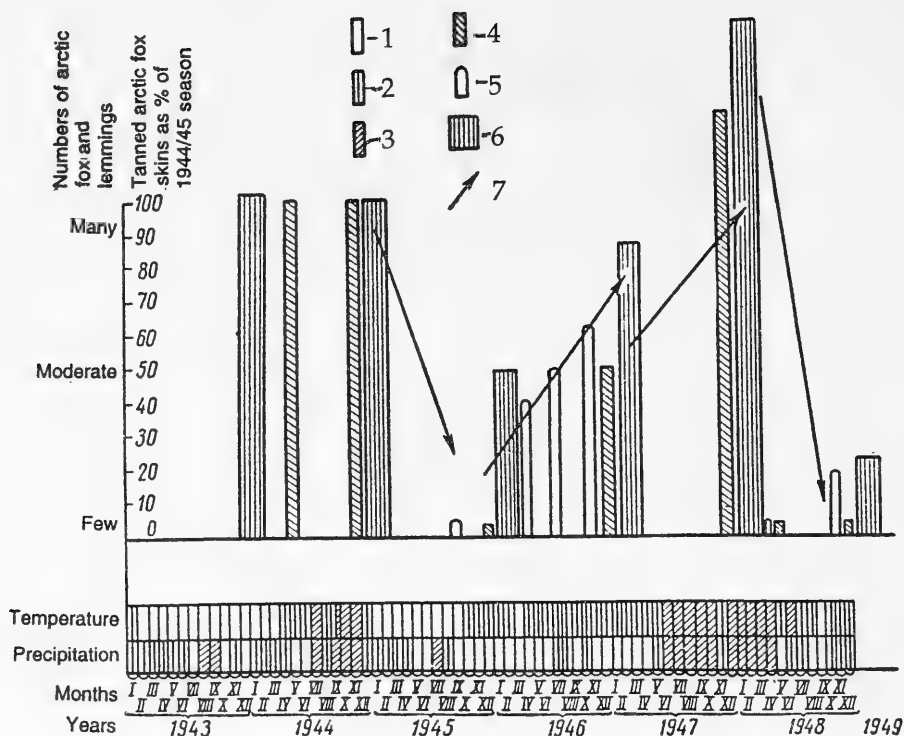
Fig. 91. Tanning of arctic fox skins in the Soviet Union as an index of fluctuations in the numbers of the species (A.F. Chirkova).

40% of the burrows were occupied by arctic foxes and reproduction proceeded well (average litters of 5–7 young) (Tavrovskii, 1958). As is seen, the numbers of arctic fox do not change synchronously in the various geographic regions and even separate places, nevertheless, great rises and falls in numbers simultaneously envelop vast areas of the European and Asiatic tundras eastward to the Lena [river]. Farther to the east, the rhythm of dynamics does not usually coincide. Only in occasional years the rise in number is observed in the area of the whole tundra zone of the Soviet Union, as it was in 1922/23, 1929/30, and apparently in the 3 years 1935/36–1937/38. A “crop” of arctic foxes in the winter of 1944/45 was noticed in the whole North with the exception of the Far East.

256 Even in the last century, the dependence of the numbers of mainland arctic fox on the abundance of lemmings, as the main food of arctic fox, was noted. At the present time, it has been convincingly shown that the massive appearance of lemmings stimulates reproduction in the arctic fox only when it takes place in the preceding autumn and winter (subnival reproduction of rodents). In the whole north of the Soviet Union, during the period 1944–1948, there can be traced a clear dependence of reproduction, migrations, and development of epizootics, and, as a result, the status of the numbers of arctic foxes, on the abundance of lemmings in the preceding autumn and winter, and of these rodents on the characteristics of weather in the course of different seasons of the year (Fig. 93). The value of these interrelationships and governing rules allows one to make a prognosis of numbers and population status of arctic foxes some months before the beginning of the harvest



255 Fig. 92. Variations in relative numbers of the arctic fox in the tundras of the Soviet Union over 5 years—1944/45–1948/49 (from Chirkova, 1955): 1—low number; 2—number below average; 3—average number; 4—number above average; 5—high [number].



256 Fig. 93. Weather condition, reproduction of *pestrushek** (lemmings) and number of arctic fox in the tundras of Yamalo-Nenetsk zone during the period 1943–1949 (from Chirkova, 1955).

1—numbers of arctic fox; 2—numbers of lemmings; 3—tanned arctic fox skins; 4—prognosis of the number, based on sum of indexes; 5—favorable weather (precipitation, temperature); 6—moderate [weather]; 7—unfavorable weather (for lemmings).

season (Dubrovskii and Romanov, 1935; Romanov and Dubrovskii, 1936; A. Romanov, 1941; Chirkova, 1951, 1955).

Migrations have great significance in the dynamics of arctic fox numbers. As stated above, through this, emigration of huge numbers of the animals from the tundra zone and their appearance in the taiga zone and on the Arctic Ocean, takes place. Latitudinal migrations of arctic foxes in some regions, for example, in Kanino-Timan tundra at the time of great increase in their numbers, increases the total "crop" of arctic foxes, while the local groups of the animals remain small (Bashkin, 1940, Shibanov, 1951). On the

*Local name—Sci. Ed.

Commander islands and the sea coasts of the mainland tundra in the east and west of the range in the USSR, where the food supply in the form of marine flotsam is relatively permanent, the number of arctic fox is more stable and changes less in the various years.

Exploitation [for fur] also reflects numerical dynamics. Intensive trapping out of arctic foxes in years when they are abundant, increases the probability of survival among the remaining animals. Increased take of arctic foxes in the years when they are few in numbers is not rational, since it decreases the producer group. Hunting of arctic foxes in the burrows in the second half of winter, when they are preparing to breed, is particularly harmful. Rational utilization, taking into consideration the numbers of arctic foxes and the conditions of their existence, may favorably influence the population, increasing its productivity.

Blue foxes, common in regions with mild climate, and extremely rare in mainland tundra (a tenth and a hundredth part of the percentage among white arctic foxes; Paramonov, 1929; Lavrov, 1932; Zubkov, 1936 and others), are more often observed in years of abundance of the species. In Canada, blue arctic foxes also occur in larger quantities in years of massive reproduction of white arctic foxes (Hewitt, 1921).

In Canada, massive purchases of skins are repeated each 3–5 years, 4.2 years on the average. The catch of arctic foxes in individual years decreased 8–9 times (Seton-Thompson, 1909–1925; Hewitt, 1921). Co-occurrence of the year with an abundance of lemmings was established in both Norway and Canada (Elton, 1931, 1931a). The numerical dynamics of the arctic fox in northern and regions of the Arctic and sub-Arctic zones of America differ. Increase in numbers of arctic foxes over large territories in Canada was noted in 1933/34, 1937/38, 1941/42 and 1945/46, and massive reproduction of lemmings—in the same or the preceding years (Elton and Chitty, 1937, 1938, 1939, 1940, 1941, 1942, 1943, 1950).

Stocks of arctic fox in Greenland are subjected to strong annual fluctuations depending on the arrival of spring, meteorological conditions which are determined by the amount and character of the passing of huge masses of drifting ice from the Arctic Ocean to the south along the shores of the island (Vibe, 1959).



Fig. 94. Track of an arctic fox on damp sand. Khatanga. Photograph by A.F. Chirkova.

*Field characteristics.*⁵⁹ The narrow paws of arctic fox leave tracks similar in form and dimensions to those of the red fox, but somewhat more blunt (Fig. 94). On the firm snow of the open tundra, the arctic fox moves about freely, but in the soft snow of the forest zone it sinks in. Due to its highly fluffy paws, the contours of winter footprint are somewhat diffuse. The length of the track of the fore limb is 5–7 cm and of the hind, 5–8 cm. The track of female is smaller than that of the male. The load on 1 cm² of the supporting surface of the limbs is 40–60 g.

The tracks of all four paws are sometimes distributed separately or in pairs (Fig. 95). The usual movement of the arctic fox is a slow trot or easy gallop with the stride length from 45–50 cm to 100 cm or more. When pursued, the arctic fox develops greater speed. In times of fattening it, like the red fox, very thoroughly

⁵⁹Middendorf, 1869; Nosilov, 1909; Cherskii, 1919–1920; Formozov, 1929, 1946, 1959; Barabash-Nikiforov, 1937; Dubrovskii, 1937, 1940; Tyulin, 1938; L. Popov, 1939; Rutilevskii, 1939; Shastin, 1939; A. Romanov, 1941; N. Dement'ev, 1955; S. Popov, 1957; A.F. Chirkova.



Fig. 95. Tracks of a running arctic fox on a snow-covered surface. Khatanga.

Photograph by A.F. Chirkova.

searches all bushes, hummocks and projections above the soil surface. During the hunt, the arctic fox changes its gait, now slowly sneaks up, sniffing a track or following the prey at a distance, now creeping on its belly, then quickly glides forward or makes a sudden jump to overtake the victim. The arctic fox seeks out lemmings along their runways, senses and hears through the mass of snow,

vigorously digging them out even in the compressed snow up to 1 m deep. At the capture site, only traces of blood or the stomach of the rodent remain. On Belyi Island in 1936, 49 holes 10–15 cm deep each were dug in the snow by an arctic fox in an area of 100 m², who made 3 passages in 50 cm reaching the soil itself; for all of this only one lemming was caught.

In distinction from the red fox, the arctic fox makes broad trails, especially during mass movements along the seashore and
259 river banks. On Novaya Zemlya, in years with abundant arctic foxes, one may, according to Nosilov (1909), travel by horse along their trails. On ice, the tracks of [polar] bear are often accompanied by the tracks of the arctic fox (Vrangel', 1841; Kirpichnikov, 1937 and others).

In the second half of winter, double and triple common trails and sometimes even tracks of four animals running together are often encountered. Traces of mating and fighting most often may be seen in the Lena-Khatanga territory in February; at this time, burrows emptied of snow are found. In the tracks of females, mucous secretions are met with—signs of estrus. After mating, arctic foxes lead a secretive way of life, and signs of their activity are rarely encountered at that time. With the bright sun of spring, the white arctic fox is difficult to distinguish on the snow. On the contrary, the blue arctic fox looks almost black.

The breeding burrows are recognized by their well-worn* exits, the trampled vegetation, the digging and trails of the young arctic foxes, and the abundance of droppings and the remains of food. The presence of young in the burrow is betrayed also by the intense odor. Arctic foxes may be revealed by tapping on the soil surface above the burrow; young arctic foxes reveal their presence by short barks at such a time, while adults remain quiet. By the number of active entrances, one can judge the number of young.

At the end of summer, after the dispersal of the litters, and in autumn at the time of migration of the arctic fox, the river banks and fast shore ice become dotted with their tracks. Before the rivers freeze or formation of fast shore ice in the sea, tracks of the animals are concentrated in a narrow 1–2 m strip along the edge of the water. With the growth of fast shore ice, the arctic foxes move

*The Russian word *obglazhennyc* literally means either "picked," "gnawed," or "smoothed," "worn"—Sci. Ed.

with it farther away from the shore. They move out onto the thinnest ice, and only the sound of the ice cracking makes the arctic fox instantly jump backwards; during this, it raises its pads like a cat, fearing to wet them. To the side of the general path, only tracks of individual arctic foxes are observed, running hurriedly to a ravine or to the thicket of bushes, in order to search for food. From the tracks, one may see how the arctic fox can, with a sudden jump punch a hole in the thin ice to catch a small fish under it. A dog following an arctic fox onto newly-formed ice often falls through, while the arctic fox, being lighter in weight, only slips.

The sense organs in the arctic fox are very well developed. The arctic fox can hear the movement of the small rodents under snow from some meters; it can react to bait at a distance of 300–400 m and run precisely in the required direction. It can see willow ptarmigan far away, entirely invisible on the white snow cover of the flat tundra. The sense of smell is excellently developed in the arctic fox; it can scent a capercaillie in the snow at 100 m. When the animal seeks food, its head hangs down and the nose “traces” the path. In its absorption in the search, especially when young, the arctic fox often does not pay any attention to surrounding objects and approaches a stationary human to within 2–3 m.

The arctic fox does not belong in the number of silent animals, and gives voice in various situations. The sounds given by it are quite varied. The usual cry of the arctic fox resembles that of a dog's bark, but more hoarse, deep and husky. An arctic fox hidden among rocks grumbles “urin-urin”. Caught during migration, sitting in a sack, the arctic fox gives a cry “ugkhu-ugkhu” when approached by a human. During the time of rut, females howl, yelp and squeal. When young arctic foxes disperse from the burrow prematurely because of lack of food, the agitated parents call them with a cry similar to that of the swan; this is most often heard at dawn. Hunters say “The arctic fox coos”; such a cry is considered to be a forerunner of migration.

On Novaya Zemlya, in the autumn of 1887 and 1888, the bark of arctic foxes was often heard at the time of migration. While running it might pause, and, raising its snout, it barked not strongly, but “complainingly”. Arctic foxes also howl while running in winter on lake ice. Judging from everything, howling in arctic foxes is related to deficiency of food. (A. Ch.).

Practical Significance

The arctic fox is one of the valuable species of fur-bearing animals. The USSR occupies first place in the world in the size of its fox fur trade. In pre-revolutionary times, tens of thousands were obtained in Russia and about 3/4 of the harvested catch was sold in internal fairs, of which the chief were the Irbit'sk, Nizhegorod and Yakut'sk. Part of the skins were exported to China, Manchuria, Japan and America. There is information on the exportation of great quantities of arctic fox skins from some regions of Russia. In the middle of the 18th century, according to Steller, more than 7000 arctic foxes were caught during three wintering periods on Bering Island. In 1825 and 1826, 140 thousand skins were exported from Turukhansk territory; from Mangazeya, up to 40 thousand. Individual authors refer to this in connection with the decline in the harvest of arctic fox. The decline in catch of arctic fox was particularly sharp in the last years of the Tsarist government.

Organized exploitation of arctic fox in the USSR began in 1922 (Paramonov, 1929; Guber, 1939; A.F. Chirkova). During the last 35 years, tanned arctic fox skins in the USSR consisted of an average of 78 thousand per year, ranging from 35 to 128 thousand. From 1946/47 to 1958/59, the average amount of skins tanned in a year increased to 81 thousand. This was promoted by the utilization of new areas, provision of supplemental feeding* of animals, the taking and holding in captivity of migrating arctic foxes, and also the rationalization of methods and tools of exploitation.

As regards the price of furs, before the October Revolution, the arctic fox occupied second to fourth place after squirrel, sable and red fox, depending on the "harvest" (Nosilov, 1909; Guber, 1929; Chirkova et al., 1959). For the last ten years, the arctic fox stands in second to third place, providing 15% of the price of furs tanned in the USSR, while in the tundra zones—up to 90–99%, and representing the main object of hunting trade for native peoples of the Far North. The most valuable white fox fur is obtained from the Yenisei tundras, Yakutiya and Novaya Zemlya. The main regions of exploitation are the Ob', Yenisei and northern Yakutiya; during
 261 the last 20–30 years they provided 30, 25 and 23% respectively of

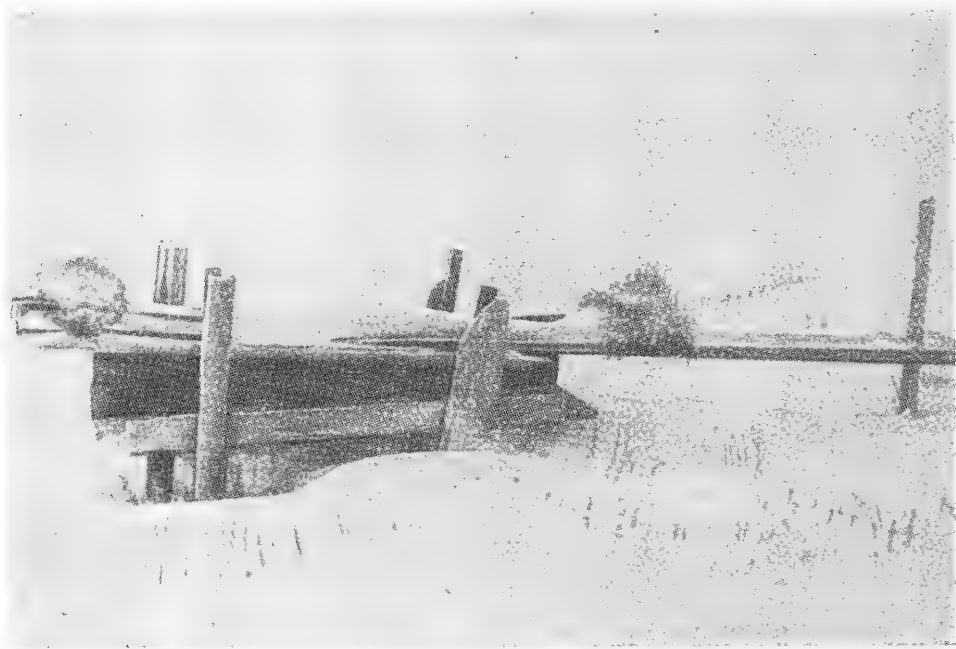
*See footnote, Table 25—Sci. Ed.

all of arctic fox production in the USSR. Arctic foxes caught in northern Arkhangel'sk district (14%) and in the Far East (7%) are fewer.

During the above-mentioned 30–35 years, an average of 5.8 arctic foxes are caught annually in an area of 100 km² of the tundras and forest-tundras in the Nenetsk and Yamalo-Nenetsk national regions, in Krasnoyarsk territory—3.2; in Yakutiya—3.7, and in the Far East—1.2. At the same time, in the territory of the *kolkhoz* [collective] “Krasnyi Oktyabr' ” [Red October], on the Kara Sea coast, in the 1950's, an average of 19 arctic foxes were caught yearly, and in years with a good “harvest”—up to 30. In the end of the past and at the beginning of the current century, on the Commander islands, up to 13 arctic foxes per 10 km² were captured by means of drives (through the year). Success of the harvest of arctic foxes differs greatly by year. One hunter taking 10–20 arctic foxes in a season of moderate numbers, may catch up to 100 or more animals in years of abundance. Individual hunters in north-eastern Yakutiya obtained up to 176 arctic foxes, on Wrangel' Island—up to 125, and in northeastern Bol'shezemel'sk tundra—more than 200 arctic foxes per season.

In connection with the sharp variation in the numbers of arctic foxes, there arose the necessity for an organized service to estimate the “harvest” and to make a prognosis of arctic fox number. It was organized by the Administration of Glavsevmorput' [Main Northern Sea Route] in 1935, when the first general prognosis of changes for the whole North was given, which proved to be true for a considerable part of the USSR (Dubrovskii and Romanov, 1935; Romanov and Dubrovskii, 1936; Guber, 1939). The institute of the hunting industry (VNIO) [All-Union Scientific Research Institute of Hunting], in the course of a series of years, presented an analysis of the condition of the populations for the tanning organizations, and gave a prognosis of the number of arctic foxes in all sectors of our Far North; they were verified in the overwhelming majority of cases (Chirkova, 1955).

At the present time, the main methods of arctic fox capture combine old ways and equipment with new techniques. In some places, the old method of capture are used; driving with [rein]deer, barriers on the banks of rivers and the sea, but they are additionally equipped with new types of deadfalls, food-baits, the newest jaw-traps and explosive weapons. Wooden deadfall traps are mainly used in the Taimyr National Region and in Yakutiya, and rarely in



260 Fig. 96. *Slopets*, or deadfall, for arctic fox (side wall open) in northeastern Bol'shezemel'sk tundra (European North). Photograph by Yu.V. Rybalkin.
[See also Fig. 97.]

other tundras (Figs. 96, 97). They represent a narrow corridor with a bait in a box.* The arctic fox is killed by a log, hung above the corridor. Deadfalls are located along the seashore, river banks and in other sites, where the arctic foxes are most frequently encountered. On the Taimyr peninsula, trap-lines extend from the border of the forest in the south northward deep into the tundra for 100–
262 150 km and more. At the present time, improved traps are being deployed, especially portable traps—irreplaceable equipment for harvest in sparsely populated tundras. The steel jaw-traps occupy second place among the implements of trapping. They serve as the main trap used for harvesting arctic fox in the western tundras and in northeastern Siberia.

*The Russian word is *strozhka*, literally “lodge” or “hut”—Sci. Ed.

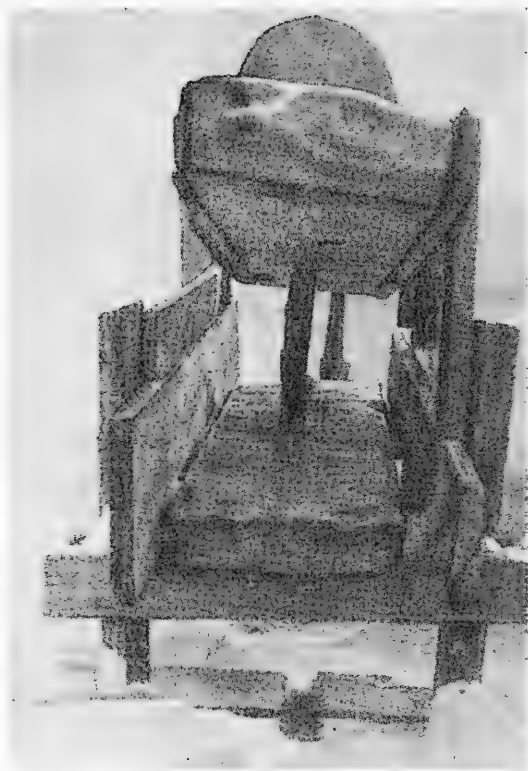


Fig. 97. View of deadfall from the front. Photograph by Yu.V. Rybalkin.
[See also Fig. 96.]

A pot drive*, or “*tolar*” is employed on Yamal and in the tundras of the European North. In it, from 2–6 tens of hunters on reindeer teams participate, traveling in a spiral over open, comparatively level territory of an area of some tens of square kilometers. Arctic foxes, fearing to cross the fresh trail of the deersled, gather in the center of the site around which the harvesters are traveling. The hunters kill the arctic foxes with guns, or even sticks. In years of abundance they take up to 150–200 arctic foxes in a circuit. The method of *tolars* on foot also exists. Sometimes, the arctic foxes are driven on to promontories of the seashore or into nets that are set up (Romanov-Il’inskii, 1958; Skrobov, 1963).

*The Russian phrase is *zagon kotlom*—Sci. Ed.



Fig. 98. Blue arctic foxes arrived for supplemental feeding. Mednyi Island. December 1953. Photograph by S.V. Marakov.

Arctic foxes are frequently shot from a blind, during solitary stalks on [rein]deer or horses, with dogs or in an accidental encounter. Harvest of the arctic fox on the seashore during the time of autumn migration is permitted only in an organized arrangement for the sake of keeping the animals in captivity until full pelage. Forbidden everywhere is *klyapts**, digging out animals from burrows, baited crossbow-traps, and baits poisoned with strychnine, corrosive sublimate [mercuric bichloride], nuxvomica or poisonnut, tormentil and other poisons. The modern method of catching live arctic foxes by means of food-supplied live traps is employed mainly in the island enterprises, but has begun to be used in mainland tundras. In Bol'shezemel'sk tundra, portable food-supplied live traps

*Meaning not clear; perhaps a kind of trap—Sci. Ed.

of simple construction are used (Boitsov and Pereleshin, 1934; Freiberg, 1939; Skrobov and Kozhevin, 1955, 1957).

263 The best methods for catching the arctic fox are snares and traps based on the employment of lures and baits. Lures for the arctic fox may be visual, food, scent and mixed. Each object on the snowy surface of the tundra can be seen from afar and attracts the arctic fox's attention, and therefore hunters drive into the snow pieces of deer-antlers, chocks, set up piles of stones, and pile up hillocks of earth or snow, etc. Food lures are very varied. However, fresh carcasses of lemmings, grouse, hares and spoiled eggs are a continual preference of the tundra population of arctic foxes. Arctic foxes of the coastal regions prefer fresh fish and fat of marine animals. Blood of freshly-killed [rein]deer and other animals acts as a good lure. In order to attract arctic foxes to hunting areas before the beginning of the harvest, they place baits such as carcasses of common seals, ringed seals, white whales and other animal and fishing industry wastes to which arctic foxes are attracted to feed. This considerably increases the catch.

In previous times, the hunt for arctic foxes continued through almost the whole year. In the middle of summer the young *nornik* were dug out of burrows for nursing. The regular harvest of skins began at the end of summer, taking in abundance *krestovatik* [cross], *sinyak* [blue] and *nedopesok* [premature], and the catch continued to April. In years with an abundance of migrating arctic foxes, a coastal harvest existed, when 5 to 10 or more animals not in full pelage were taken per night. In such years, more than 50% of the harvest consisted of "nevykhodnye"* arctic foxes. In the past, arctic fox skins were given as tribute, from each Nenets two arctic foxes were taken, while from Evenk and Dolganin—four. As a quantitative unit of exchange, among the Vaddeevsk Samoyed, 20 arctic foxes were equal to one boat.

From the first years of the Soviet state, the catch of *nevykhodnye* arctic foxes—*nornik* [burrow dwellers], *krestovatik* [cross], *sinyak* [blue] and the spring "gagara" [loon] was forbidden. A harvest season was established from the middle of November—beginning of December, to the beginning or end of March (in various regions).

*Literally "unfinished", i.e. immature—Sci. Ed.

An arctic fox industry is conducted on islands surrounded by unfrozen seas (Boitsov, 1937; Il'ina, 1949–1950 and others). Bering Island supplied arctic fox to Andreyanov Island (Aleutians) which belonged to Russia at that time (Khvostov and Davydov, 1810–1812). At the end of the eighteenth century, G.L. Pribylov [Pribilof] exported 8,000 skins of blue arctic foxes from Georgii and Pavel [St. George, St. Paul] islands in two years, and only after that arose the question of the preservation of these animals there. It was of great practical importance to organize an intensive arctic fox industry on the Commander islands, where blue arctic foxes occur. In 1741, when Bering visited these islands, blue arctic foxes thrived there in “incalculable packs”. Steller killed tens of arctic fox with an axe in a day, and used the skins of the animals to cover the roofs of the earthen huts. At the end of the 90's of the nineteenth century, 1.5 to 2.5 thousand arctic fox skins were taken annually from the Commander islands. In the beginning of the twentieth century, as a result of overharvest, drives began to be allowed only in alternate years, preserves were allotted, counts of arctic foxes were promoted to determine the number allowed to be killed, and the permissible period of capture was shortened to 2–3 weeks. As a result of many years of selection, white arctic foxes, individuals of which appeared on Bering Island particularly often, were exterminated. Only under the Soviet government in the 20's was winter supplemental feeding introduced and in the 30's, in summer as well. Food-baited live traps began to be used and continuous zootechnical selection conducted. It is supposed that the arctic fox population on the Commander islands can be increased to 40 thousand head. In the 20's, attempts were made to transfer arctic foxes to the small coastal islands of the Pacific Ocean and to the Solovets (united in winter with the mainland by an ice bridge), with the aim of organizing there an island blue arctic fox industry. All of these ended unsuccessfully.

264 Experiments on supplemental feeding of the arctic fox showed the great importance of this measure not only for islands, but also in the mainland tundra on several farms in isolated territories. Supplemental feeding must be begun during the time the litters are still in the burrows—at the first signs of the disappearance of natural food in spring, summer and early autumn, to inhibit the arctic foxes from migrating, and also in winter in places where animals concentrate and before the beginning of rut.



Fig. 99. Blue arctic fox lying in rocks. Bering Island. October 1958.
Photograph by S.V. Marakov.

Intensive arctic fox farming on islands has been conducted in North America for the past century, based mainly on wastes of the marine animal industry (Suvorov, 1927; Boitsov and Pereleshin, 1934; Boitsov, 1937). As already mentioned, the first release of blue arctic foxes on the Aleutian chain was done by Russians in the middle of the eighteenth century already, and on the coastal islands of Alaska in 1835, and American trading voyages for this activity were undertaken only in 1885. Supplemental feeding of arctic foxes on the Pribilof islands began in 1896; later other measures were carried out. Concentrations of arctic foxes here attained very high densities; up to 500 arctic foxes occurred for each food-baited live trap.

Commercial raising of arctic foxes in state animal *sovkhoz** was begun in the USSR in the 30's. Raising the blue form was introduced rationally due to their great value. Cage raising of blue arctic foxes, developed in a series of European countries and in North America, past through a crisis in the post-war years as a result of the creation of a mode for short fur. At the end of the 1950's, some rise in demand was again noted, though public taste turned to white and light-blue arctic foxes.

The proportion of white arctic fox in the fur export of USSR reached 7.3% (1933). Before the Great Fatherland War**, blue arctic fox was priced significantly more expensively than white in the world market, and the darker, the higher, but in the Leningrad fur auction (1961), white arctic foxes sold with higher prices than the blue, and among the latter, the more expensive skins were of light color.

265 World production of arctic fox fur (Brase, 1925) in the period 1907–1909 averaged 116.0 thousand skins, of which 105.0 thousand were white, and in 1923–1924, 204.0 thousand skins, of which 166.0 thousand were white. North America contributes on average about 1/3 of the skins of white arctic fox. In the 20's and 30's, from 18 to 72 thousand skins were bought in Canada, an average of 44.9 thousand. In Greenland at the end of the last century, an average of 1.5 to 2.0 thousand arctic foxes were caught every year. In Spitsbergen in the 19th century, the arctic fox was exploited especially intensively. In the 20's of the current century, only 100 blue and 250 white arctic foxes were obtained annually. At the present time, great attention is paid there to the preservation of arctic fox (Soyrinki, 1958; Bergman, 1961).

Arctic fox meat has an unpleasant odor, but on Yamal many people ate it (Nosilov, 1909; N.N. Spitsyn). At the present time, the question of the specific activity of the fat of arctic and red foxes as a medical dietary treatment against tuberculosis and liver diseases in humans arises (Mironov, 1953).

Arctic fox has a negative significance as a disperser and transmitter of tundra rabies. In years of outbreaks of this disease, many sled- and herd dogs and reindeer are bitten by arctic foxes, are infected and die. However, the frequency of disease transmission

*State farms—Sci. Ed.

**World War II—Sci. Ed.

by arctic foxes may be exaggerated due to insufficient study of the significance of rodents and other animals of the tundra. Since echinococcosis, trichinosis, diphillobothrosis, opistorchosis and other helminthoses are found in arctic foxes, the possibility of the transmission of these diseases to humans is not excluded. (A. Ch.).

Genus of [Common] Foxes

Genus *Vulpes* Oken, 1816

1775 *Vulpes*. Frisch. Natur-Syst. d. Vierfüß. Thiere, p. 15. By decision of the International Committee on Nomenclatural, this work was considered to have no nomenclatural significance.*

1816 *Vulpes*. Oken.* Lehrb. d. Naturgesch., 3, Th. 2, p. 1033, 1034. *Vulpes communis* Oken = *Canis vulpes* Linnaeus.

1839 *Cynalopex*. H. Smith. Jardine's Nat. Library. Mamm., 25, p. 222. *Canis corsac* Linnaeus (V.H.).

Species of medium and small size.

Skull light and slender, elongated, with widely situated zygomatic arches, and low (height in occipital region less than 1/3 of condylobasal length). Skull sculpturing is weakly defined, sagittal crest not developed at all or weakly defined only in posterior part of the parietal bones. Facial part light and slender, considerably, sometimes very strongly elongated and much longer than braincase; its length from the posterior wall of infraorbital foramen to posterior edge of the canine alveoli greater than skull width above the canines, while distance from line connecting ends of supraorbital processes to anterior end of premaxillae significantly greater than that to upper edge of occipital foramen.

Interorbital (frontal) region flat, not swollen between supraorbital processes—here a concavity (groove) is located; supraorbital processes large, dorsally somewhat concave, with small air cavities, a quite sharp edge and with apex directed somewhat downwards. Profile line of rostral part of skull grades very gradually into frontal-parietal line, not forming a noticeable, or only an ill-defined, projection; sometimes, upper profile of skull conforms almost to a completely straight line.

266 Posterior edge of tooth row reaches level of anterior edge of interpterygoidal fossa. No deep notch and projection on lower edge

*However, the International Commission on Zoological Nomenclature (1979) retained *Vulpes* Frisch 1775, while rejecting *Vulpes* Oken 1816.

of lower jaw in front of angular process.

Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42$. In some, as individual deviation it may be $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{2} = 40$. Teeth relatively small and light, with very sharp cusps and ridges. Length of upper carnassial tooth and molars $2\frac{3}{4}$ –3 times more than palatal length. Canines thin, strongly curved and very long—when jaws are closed, tips of upper canines reach or nearly reach lower edge of mandibular bone or even extend beyond it, while tips of lower canines are located above edge of alveoli of upper canines (Fig. 18). Ends of upper canines directed straight downwards; no cutting edge develops on posterior side of canine; canine surface entirely smooth. Incisors usually without accessory lobes.

Trunk long, limbs quite short, tail very long—more than half that of body, always falls below tarsal joint, and in standing animal reaches the ground. Head elongated, with long pointed muzzle. Ears long, when bent forward always reach eye, sometimes very long with pointed tip. No large bare callosity found on the rear extremities behind four bare toe pads (a small one occurs—feet covered with fur). Glandular area is found in front of the middle callosity on the fore and hind limbs.

In some, fur dense, fluffy, long and soft (northern forms), in others, more sparse and coarse. Color monophasic, in one species (red fox, *V. vulpes*) polyphasic, and, except for black phase of this species, adults do not exhibit only one color. In various species, the prevailing colors are reddish, sandy- and clayey-yellow and brown tones with silvery-white and black in the form of admixtures and black markings. Supracaudal gland well developed. Nipples 4 or 6 pairs. No marked sexual dimorphism (males are slightly larger), age dimorphism well manifested and seasonal dimorphism is sharp in some forms (northern), but is revealed almost solely in degree of fur density and length. There are two molts per year.

In general appearance, species of the genus are relatively very monomorphic, differing mainly in size. In this respect, three types occur: the relatively large red foxes (*V. vulpes*), forms of lesser size—corsac fox (*V. corsac*) and its analogues, and very small foxes of the Baluchistan type (*V. cana*). The largest forms have a

body length up to 90 cm and weight up to 14 kg and the smallest—about 40 cm in body length and hardly more than 2 kg in weight.

They are inhabitants of extremely varied landscapes—from tundras and taiga to extremely high mountains, and steppes and deserts. They prefer areas with more or less open expanses and avoid the dense thick forests. There are no regular migrations. They are monogamous, uniting for one reproductive season. Up to 13 young, usually less, born in burrows. They are carnivorous animals, feeding on small vertebrates, mainly rodents, carrion, and as an exception, on insect and plant food. Except for the breeding season, they lead a solitary way of life.

The range of the genus is very vast, located on four continents and in all climatic zones. It occupies all Europe, to North Cape and islands of the Mediterranean Sea, includes the British islands (absent in Iceland), all Africa except Madagascar, and Asia northward to the northern shores of the continent (except the northern Taimyr) and the Kolguya islands, Yuzhnye Novaya Zemlya and Belyi islands (locally wandering animals may be seen farther north; see description of red fox, *V. vulpes*) and southward to Tonkin, Yunnan, Sichuan, Assam, Bengal and India to Cape Comorin. It occupies the entire Arabian Peninsula. The range includes Karagin, St. Lawrence, Kuril, Sakhalin, Shantar and Japanese islands. Species of this genus are absent on the islands of the Bering Sea (except those mentioned).

In North America, the range extends northward to the northern coast of Labrador, Hudson Bay, a line from Chesterton (on the western shore of Hudson Bay) to Coppermine (on the Arctic coast), and farther westward on the Arctic Ocean and Bering Sea coasts. Southward, the range extends to California and northern Mexico inclusive, but does not include the southern and southeastern states of the USA from Maine to Louisiana (for details, see range description of red fox, *V. vulpes*). The range includes Newfoundland and Kodiak islands. Species of the genus are absent from the coastal belt of British Columbia and adjacent islands. Acclimatized in Australia (*V. vulpes*). In the vertical direction, they reach extreme heights. The range of the genus was not subjected to substantial reduction in the past century.

In systematic characteristics, *Vulpes* represents a more specialized group than *Canis* and *Alopex*, and the degree of specialization of some species (*V. ferrilata*, *V. cana*) is very high. Besides the

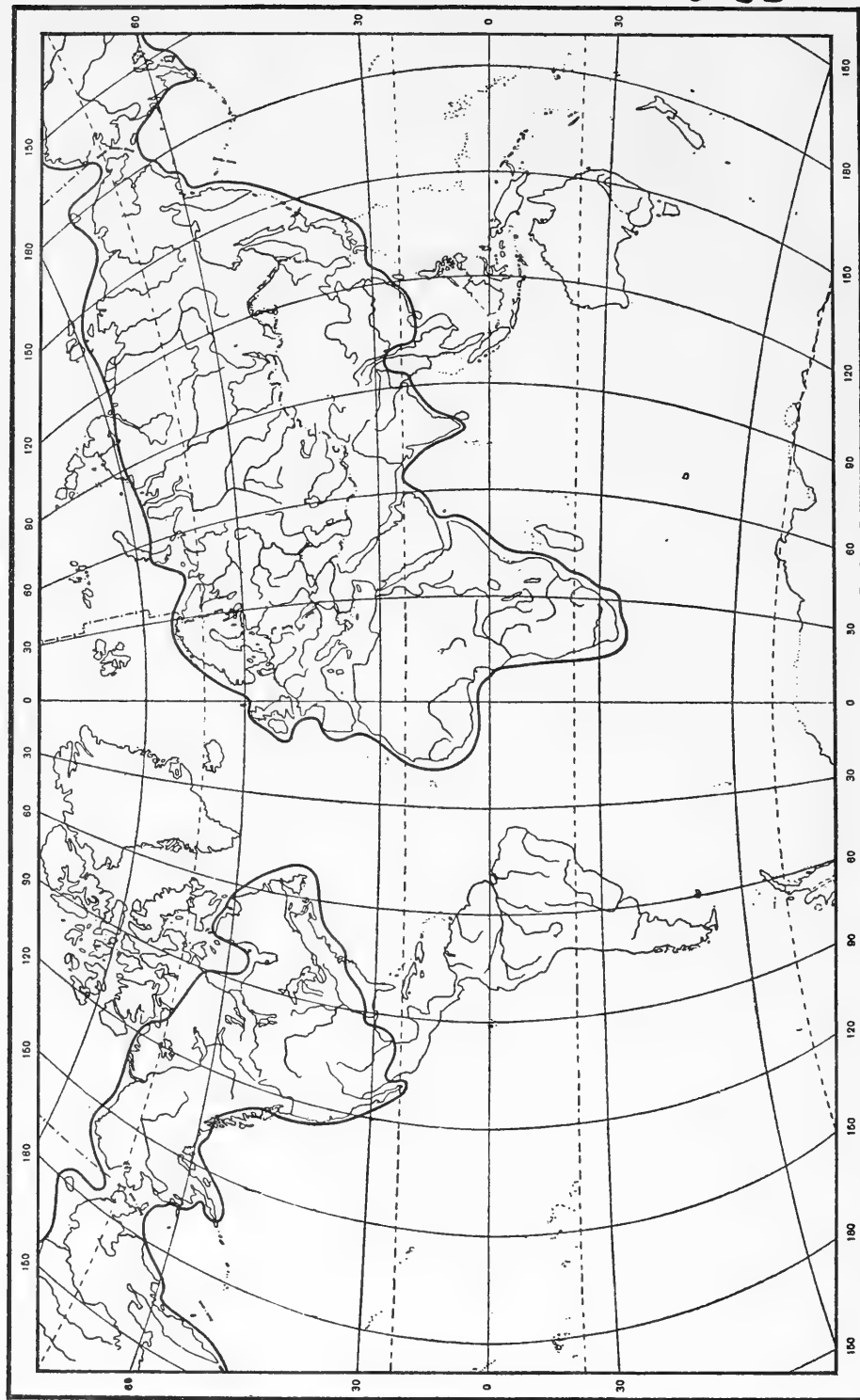


Fig. 100. Range of the genus of foxes, *Vulpes* Oken (including areas of wandering in northern Eurasia). V.G. Heptner.

close relationship to the arctic fox, *Alopex* (see above), *Vulpes* is closely related to the fennec group—genus *Fennecus*. All three genera are considered “neighboring” groups. Through *Alopex*, *Vulpes* is related to *Canis* (wolves and jackals) (see characteristics of family and of named genera). The relation to genus *Ducicyon* (American gray fox and close species), with which the described genus is sometimes associated is, apparently, more distant. Since the extreme forms of all the genera mentioned have much in common, and serve as connecting links between them, there is basis for considering all of them as only subgenera of one broadened genus—*Canis* (see the family characteristics). At the present time, however, it is still almost always considered as qualifying as independent.

The genus already was separate in the Pliocene and may have appeared even in the lower Miocene (North America). In Europe and Asia, it is known in the Pleistocene. The genus *Vulpes*, like *Canis*, probably developed from the American Mio-Pliocene group *Tomarctos*.

In the contents accepted here, the genus is quite monotypic and was not subjected to any considerable subdivision. Attempts were made to split into a separate genus the corsac fox (*V. corsac*) and unite it (sometimes also with *V. velox*) with genus *Alopex* (arctic foxes).

In the genus are 6 species: 1) red fox, *V. vulpes*; 2) corsac fox, *V. corsac*; 3) Bengal fox, *V. bengalensis*; 4) Afghan fox, *V. cana*; 5) American small fox, or American corsac, *V. velox** and 6) Tibetan fox or Tibetan corsac, *V. ferrilata*. The genus includes about 20% of the species of the family, 4 Asiatic species (*V. corsac*, *V. bengalensis*, *V. cana*, *V. ferrilata*), 1 American species (*V. velox*)* and 1 species distributed in the greater part of North America, in almost all Eurasia and in North Africa (*V. vulpes*).

The African *V. chama* and the African-Near Eastern *V. rueppelli* are sometimes included in genus *Vulpes*; however, they are apparently to be referred to genus *Fennecus*.

The fauna of the USSR includes 3 species: 1) red fox, *V. vulpes* Linnaeus, 1758; 2) corsac fox, *V. corsac* Linnaeus, 1768; 3) Afghan fox, *V. cana* Blanford, 1877, i.e. 50% of the

*In English, swift fox; *V. megalotis*, the kit fox, is often considered a distinct species as well—Sci. Ed.

species of the genus, and about 1% of the species of the USSR fauna¹.

The range of the genus covers the entire territory of the USSR, except the above-mentioned northern regions. Species of the genus are met with in all landscapes of the country.

- 269 The members of this species are useful as commercial fur-bearing animals, and in part for limiting the number of harmful rodents. In places, they cause some harm by killing useful sporting animals and birds (V.H.).

AFGHAN FOX²

Vulpes cana Blanford, 1877

1877. *Vulpes cana*. * Blanford. Journ. As. Soc. Bengal., 46, pt. 2, p. 231. Gwadar, Baluchistan (Mekran coast).
1907. *Vulpes cana* var. *nigricans*. Shitkow. Zool. Anz., 32, p. 448. Southern Tadzhikistan ("Gornaya [montane] Bukhara"). V.H.

Diagnosis

Dimensions very small, body length not more than 50 cm, condylobasal length of skull not more than 91 mm. Tail tip not white, back color gray mixed with black ripples, without reddish and brown tones, or they are very weakly developed (V.H.).

Description

The Afghan fox is a carnivore of typical "foxy" appearance, but of very small size. It has relatively short legs, elongated trunk and very long tail. Its length is considerably more than half the length of the body, and in a standing animal it reaches the ground. Head with very pointed, typically fox-like muzzle and large, wide, erect pointed ears. Their length more than half the length of hind foot.

Number of teats unknown.

¹Information on the occurrence of *V. rueppelli* Schinz, 1825 [*V. (Megalogotis) famelicus* Cr.]; Flerov, 1932] in southern Turkmeniya is a mistake.

²"Shardel" of furriers.

* Misspelled "*canus*" in Russian original—Sci. Ed.



Fig. 101. Afghan fox, *Vulpes cana* Blanf. Sketch by A.N. Komarov.

In winter, the fur is dense, fluffy, very soft and relatively quite long. Dorsal guard hairs 45–65 mm long, underfur, 35–45 mm. Tail covered with dense, long hairs (their length 65–90 mm) and very fluffy.

General tone of winter fur brownish gray, with well-developed black highlights along back originating from guard hair color. Guard hairs have black terminal portion, with a small silvery-white zone proximal it. Some guard hairs are entirely black. Guard hairs form on the skin a silvery frosting. On head, general color lighter and somewhat whitish. Well-defined blackish-brown stripe runs from corner of eyes to base of vibrissae. Light rusty frosting develops on occiput. Rear sides of ears gray in color or blackish-gray. Chin
 270 dark brown or brownish-black. On sides of the body, color considerably lighter than on dorsum, changing into pale yellow-gray. Here admixture of black guard hair is small; guard hairs have gray and silvery tips and underfur lighter than on back. Throat, lower part of neck, chest, and whole abdominal surface white, with light straw-colored tones. Extremities gray in color, more or less dark, with light rusty highlights on external side. On fore feet, black markings

sometimes present. Tail gray, with strong blackish highlights above. In region of supracaudal gland, on upper side near base, is a well-defined dark spot. Underfur is mouse-gray in color, their tips with light, or more or less intense ochreous highlights.

Individual variation in the color described above are known. It is expressed chiefly in that individual specimens are tinged especially dark gray in color without any ochreous or rusty admixture or with a very weak admixture of these tones, above all on the legs. In others, the admixture of ochreous and rusty ("foxy") tones is more noticeable, and the rusty is well expressed on the shoulders.

Summer pelage is not described. The first [juvenile?] pelage and age variation in color are not known.

The fox we are describing is very rare in collections and its amplitude of variation is poorly known. Generally, this species is, in many respects, poorly studied.

Skull resembles that of corsac fox, but facial portion relatively shorter, braincase relatively larger and more expanded. Zygomatic arches widely separated and are quite broad anteriorly, from which its general outline is more or less rounded (together with rostral portion, not forming evenly tapered clinoidal figure). Nasal bones narrow and highly tapered towards posterior end. Sagittal crest not developed, and temporal lines stand far apart from each other, forming a lyriiform figure. Molars relatively large; canines thin and long. Middle incisors without accessory blades.

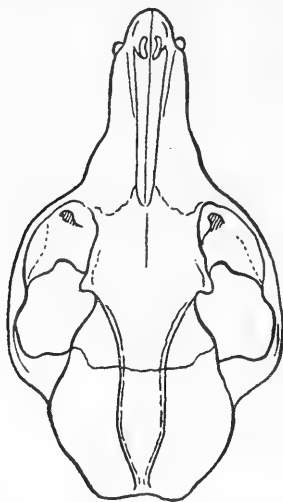


Fig. 102. Skull of Afghan fox, *Vulpes cana* Blanf. (after Pocock, 1941).

Chromosome number unknown.

Size very small—this is the smallest species of the genus in our fauna, and in the genus generally. Body length 40–50 cm, tail length 33–41 cm, hind foot about 100 mm, ear length about 90 mm.

Condylobasal length of skull, 89–91 mm; zygomatic width, 50–51 mm; interorbital width, 18–19 mm; length of hard palate, 45 mm; length of nasal bones about 29 mm, length of upper molar row, 41–44 mm; length of lower jaw, 67–69 mm; length of upper canine about 10 mm; and of lower, 8 mm (according to Pocock, 1941, and Novikov, 1956; published data are those of separate individuals; in our museums, there are no fully valuable materials).

Information on comparative sexual dimorphism in size is absent; as in all foxes, females are probably smaller than males (V.H.).

Geographic Distribution

Eastern part of Near East.

Geographic Range in the Soviet Union

This represents the extreme northern periphery of the species range. In dimensions it is insignificant and is limited to the extreme south of Middle Asia.

- 271 Reliable places of capture of the Afghan fox lie in the Kopet-Dag at the northern foot of the western part of the Sarymsakli range, 40 km from Germab, which is west of Ashkhabad (1926; Ognev, 1931), and at Bakharden on the railway line between Ashkhabad and Kyzyl-Arvat (1926; Novikov, 1956).

In the 90's*, 4 skins were brought to Moscow from "Vostochnaya [East] Bukhara", i.e., southern Tadzhikistan (Zhitkov, 1907); one of these specimens is preserved in the Zoological Museum of Moscow University in stuffed form. At that time, the possibility was admitted that these were not native, but imported from Afghanistan. The majority of later authors shared this belief.

At the present time, information has appeared that skins of this species occasionally come in from southern Turkmeniya and Tadzhikistan (Kuznetsov, 1952). According to other data (Chernyshev, 1958), "during the course of a prolonged period", not

*In Russian original, "V 900-kh godakh" [In the 900's; i.e. 10th century]. This evidently refers to the 1890's—Sci. Ed.

once has a skin of this species appeared among the fur prepared in Tadzhikistan. Thus, the question on the occurrence of Afghan foxes on the eastern shore of the Amu-Dar'ya and Pyandzh remains open and, most likely, will be settled in the negative. Southwestern Turkmeniya remains the established area of its occurrence within the borders of our country.

Apparently, one must now reach the conclusion that the Afghan fox in our country is only vagrant, appearing rarely in the Kopet-Dag and adjacent plains. This corresponds to the known occurrences of the species in northeastern Iran (Khorassan; Duruh in the eastern part of the province). It may be assumed that the species under description appears also in southeastern Turkmeniya—along the Tedzhen and between Tedzhen, Murgab and Amu-Dar'ya [rivers]. These areas lie south of the places of transience of the Afghan fox to the west [Fig. 103]. Wandering into Tadzhikistan is also doubtful because the Pyandzh and Amu-Dar'ya are probably insuperable barriers for such a small animal.

Geographic Range outside the Soviet Union

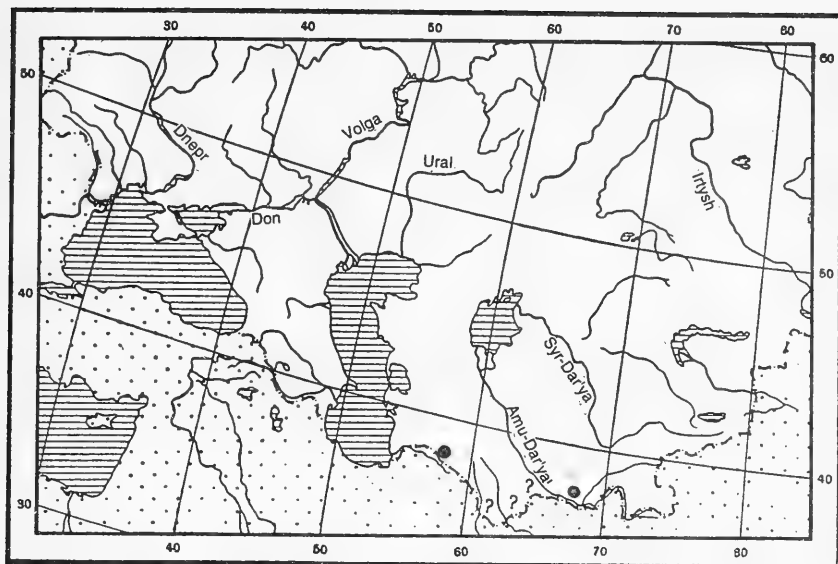
This includes Afghanistan, the northwestern provinces of India bordering Afghanistan, Sind, Baluchistan and eastern Iran, in particular Khorassan.

- 272 The range of the Afghan fox is notable for its very small size, which is unusual for a carnivore, and particularly for the species of the family Canidae. It is even smaller than the range of the relatively narrowly distributed Bengal (*V. bengalensis*) and Tibetan (*V. ferrilata*) foxes (V.H.).*

Geographic Variation

Geographic variation in this species is not described, and probably, is not manifested—its range is too small for this. Moreover, it is restricted to one natural geographic landscape region. Based on all data, the above-mentioned specimen described from “Vostochnaya Bukhara” as “var. *nigricans*” represents only an individual color deviation (V.H.).

**V. cana* has recently been found in northwestern Iran, the Arabian peninsula and Israel (Harrison and Bates, 1991), where it occupies steep, rocky habitats—Sci. Ed.



271 Fig. 103. Range of the Afghan fox, *Vulpes cana* Blanf., in the USSR. Dots designate places where animals were obtained, question marks—areas of assumed occurrence. V.G. Heptner.

Biology

There is no information whatsoever about the biology of the Afghan fox within the USSR. Data from other countries where this species lives, especially India and Pakistan, are also absent (V.H.).

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Practical Significance

In our country, the Afghan fox has no practical significance at all. As for the small number of skins, "shardel", which sometimes appear among lots of furs from Tadzhikistan and Turkmeniya, and probably from the neighboring countries (see above) they do not play any role whatsoever in fur trade. Apparently, the agricultural significance of this species is also negligible. No substantive materials are available from the other countries (V.H.).



272 Fig. 104. Species range of the Afghan fox, *Vulpes cana* Blanf. Very schematic.
V.G. Heptner.

CORSAC FOX

Vulpes corsac Linnaeus, 1768

1768. *Vulpes corsac*. Linnaeus. Syst. Nat., Ed. XII, 3, App. p. 223. Steppes between Ural and Irtysh rivers. Restricted to "Pri-Irtysh steppes south of Petropavlovsk" (Ognev, 1935).

1912. ? *Vulpes corsac* var. *nigra*. Kastschenko. Kashchenko. Ezhegodnik Zool. muzeu I. [Irkutsk] Akad. Nauk, 17, p. 393 Trans-Baikaliya.
1935. (1934)³ *Vulpes corsac scorodumovi*. Dorogostaiskii. Dorogostaiskii. Izv. Irkutsk. gos. protivochumn. inst. Sibirii i , D.V. kraya. 1, p. 47. Southern Trans-Baikaliya.
1935. *Vulpes corsac kalmykorum*. Ognev. Zveri SSSR i prilezh. stran [Animals of the USSR and adjacent countries]. 3, p. 634. Kalmytsk steppes (steppes on right bank of Lower Volga; V.H.).
1935. *Vulpes corsac turcmenicus*. Ognev. Zveri SSSR i prilezh. stran [see above] 3, p. 635 "Turkmen and Tadzhikistan semideserts and deserts". It is proposed to restrict this to: Murgab and Tedzhen districts and lowlands at foot of eastern Kopet-Dag (east of Ashkhabad). V.H.

Diagnosis

Of moderate size, larger than Afghan, but smaller than red foxes. Body length more than 50 cm but less than 65 cm, basal length of skull more than 95 mm, but less than 112 mm. Color grayish-ocherous with gray hairs, back side of ears not black, end of tail not white (V.H.).

Description

In general construction, the corsac is a typical fox and very similar to the red fox, representing itself as a reduced copy. It is also stocky and has an elongated trunk,⁴ but the tail is not nearly so fluffy and is relatively somewhat shorter. Its length constitutes half the length of the trunk or slightly more; in the standing animal, it reaches the ground. The corsac has relatively somewhat larger ears; they have broad bases and pointed tips.

Number of teats unknown.

Winter fur dense, soft and silky. Its general color is pale-yellow gray with ocherous tints. Along the middle of the back, a noticeable

³On title page, designated 1934, on cover, 1935. Appeared in 1935 (Signed by press).

⁴The idea that the corsac has longer limbs than the red fox (Ognev, 1931) is untrue.

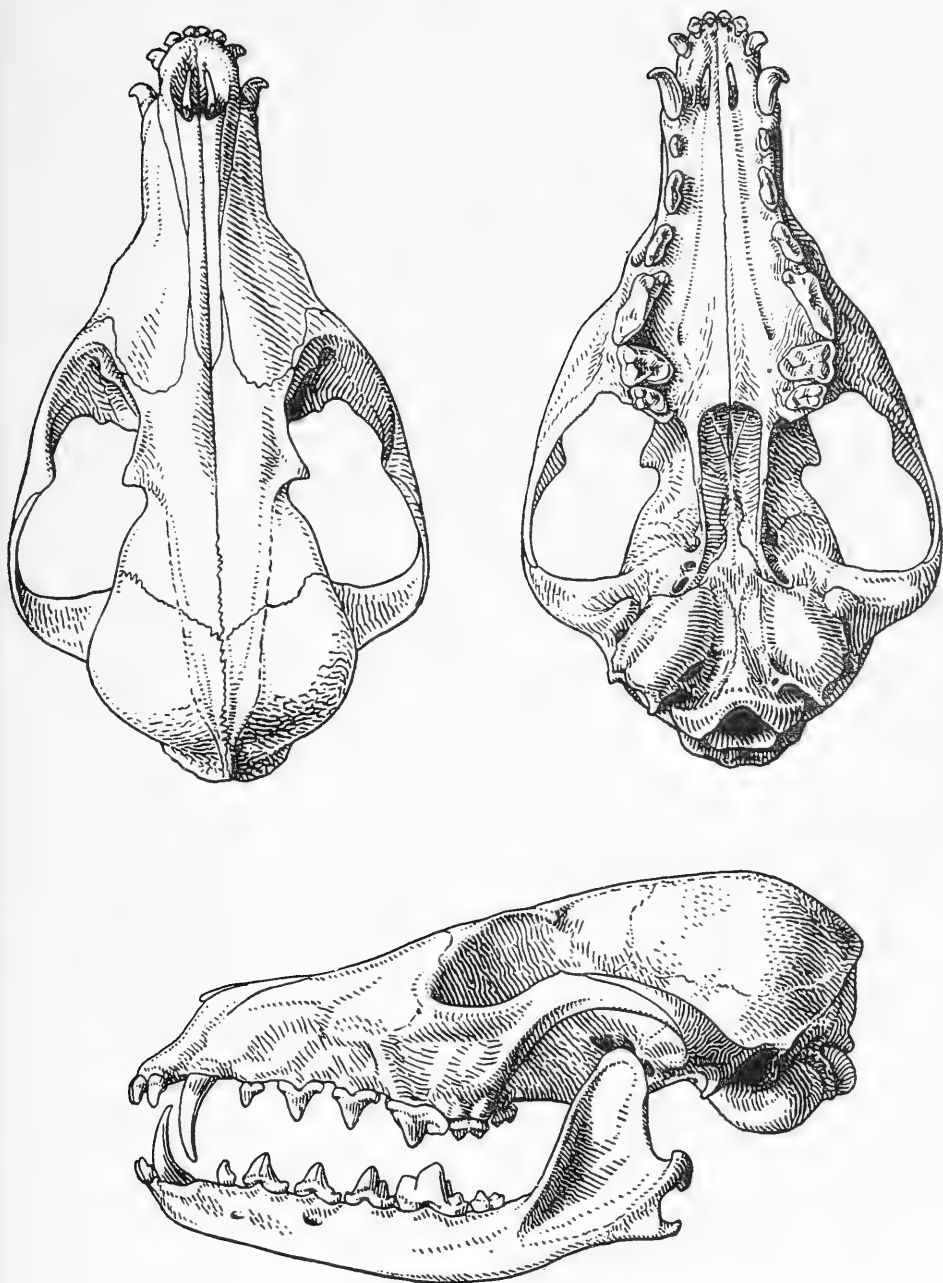
274 brownish tone and well-developed "silvery", resulting from silvery-white ends of guard hairs. Strongly developed silvery tint sometimes makes fur of the animal silvery-gray on the back. Sometimes, on the contrary, brownish tone quite strongly developed. Shoulders same colored as on dorsum. Side also with same tone, but considerably lighter. Lower surface of body, including chest and inguinal region, white or with light yellowish frosting. Fore legs light-yellow anteriorly, laterally rusty-yellowish; posteriorly, same color but paler.

Head grayish-ocherous or brown in color, darker on forehead. Around eyes color lighter, a dark field of triangular form between anterior corners of eyes and upper lip. Around mouth, on throat and along lower neck, color white with weak yellowish tint. Rear side of ear ocherous-gray or reddish-brown, bordered anteriorly along edge of ear in white, interior of ear pinna covered with yellowish-white hairs.

Tail covered with dense, fluffy hairs, and has a dirty dark-ocherous or gray-brownish general tone. On dorsal side it has blackish tinge; on basal half—6–7 cm from base in region of supracaudal gland, is found a dark spot. At base, brownish tone noticeable. Lower side pale. Tip of tail dark, usually almost black. Underfur



Fig. 105. Corsac fox, *Vulpes corsac* L. Sketch by A.N. Komarov.



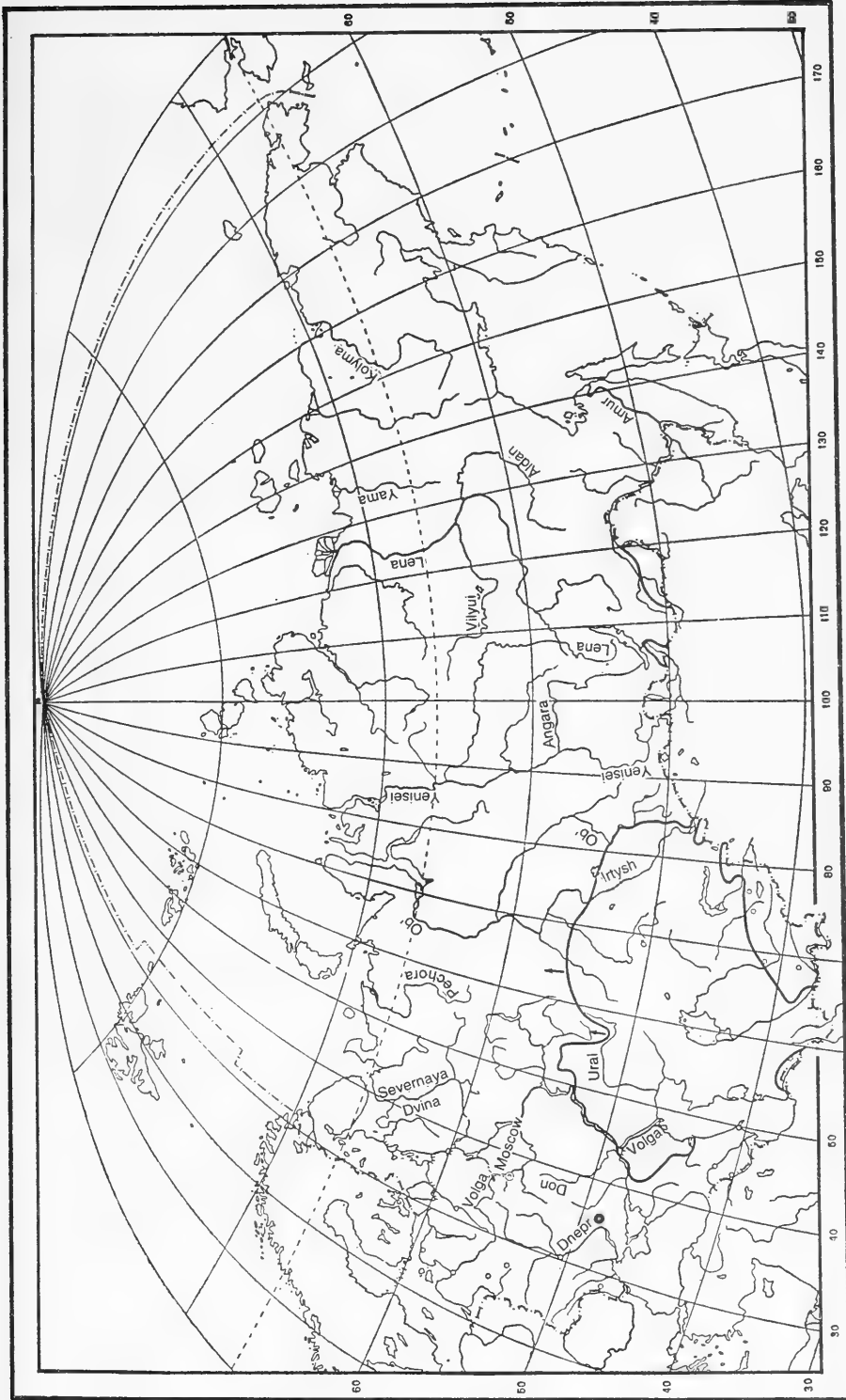
ash-gray, brownish at ends or slightly rusty. Guard hairs gray at base, white at tip, pale-brown in middle. Individual guard hairs have two dark zones with an intermediate white one.

Summer fur differs greatly from winter—it is short, sparse and coarse; tail hairs are also considerably shorter. In this fur, the corsac fox looks wiry and long-legged, with a large head. General color is more even—back and sides are nearly undifferentiated, dirty-ocherous or dirty-sandy, dull. Gray hairs are not developed in summer.

There is no sexual dimorphism in color.

In general, the skull of the corsac fox resembles that of the red fox, but, irrespective of the smaller dimensions, differs from it in many essential characteristics. In general appearance the skull is much shorter and broader and not at all elongated. The general outlines of the zygomatic arches and rostral region are reminiscent of a broad wedge—zygomatic arches are very broad posteriorly, and the skull in the region of the infraorbital foramen is broad, and not as compressed as in the red fox. Therefore, the line of the zygomatic arches merges into the line of the rostrum more gradually, without such a break as in the red fox. The rostral region is relatively short—the ratio between the length of the nasal bones and the length of the distance between their posterior end and the posterior-most point of the occipital region, is 1 : 1.6–1.8.

277 The braincase protrudes behind the transverse line passing through the articular condyles of the lower jaw for a shorter distance than in the red fox. The general volume of the quite convex and swollen braincase is relatively greater than in the red fox. It is comparatively short, but widened posteriorly. The line of the upper profile is straighter. The occipital crest is weakly developed, the sagittal, very poorly and 10–15 cm in length. The temporal lines come off of the postorbital processes almost parallel, and very gradually narrow posteriorly, uniting with the sagittal crest. They outline a wide lyriiform or triangular expanse on the frontal and parietal bones. Orbits are relatively large—their greatest height is equal to or more than the width of the interorbital region. Paraoccipital processes are weaker than in the red fox—their ends do not reach, or only just reach, the level of the lower edge of the auditory meatus. The length of the lower jaw symphysis is 4.5–6.5 times shorter than its greatest length.



276 Fig. 107. Distributional limits of the corsac fox, *Vulpes corsac* L. in the USSR. Arrows show direction and place of movements. Dot refers to place of especially long movement in the west (Pavlograd). V.G. Heptner.

Canines and carnassial teeth are comparatively stronger than in red fox. When the jaws are closed, the tip of the upper canine reaches the lower edge of the mandibular bone, the apex of the lower canine extends beyond the edge of the alveolus of the upper. Sometimes, as a form individual variation (age?), reduction of the second lower molar is observed and the dental formula becomes

$$I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{2} = 40.$$

Other than size, there are no sexual differences in the skull. Number of chromosomes unknown.

Only approximate body size of the corsac fox is known, since the data published are those of individual measurements of animals "in the flesh". Data on the skull dimensions are somewhat more, but the material is very uneven.

Body length, 50–60 cm; tail length, 25–35 cm; height at shoulder, about 30 cm; length of ears, about 8 cm; length of sole of hind foot, about 11 cm.

Greatest length of skull, 102.2–124.0 mm; condylobasal length, 98–118.1 mm; zygomatic width, 57.5–71.1 mm; skull height in region of auditory bullae, 39.0–45.7 mm.

Sexual dimorphism in size is almost not expressed, and apparently males average only slightly larger than females. The belief sometimes reported, that females are larger than males, is incorrect (V.H.).

Geographic Distribution

Flat steppes and semideserts, in part deserts of Asia and Southeastern Europe.

Geographic Range in the Soviet Union

This is relatively small, but constitutes a considerable part of the western range of the species. It occupies the steppes and deserts of the southeastern European part of the Soviet Union, northern Caucasus, Kazakhstan, Middle Asia and Trans-Baikaliya. It is divided into two parts isolated from each other, uniting outside the borders of the USSR.

The main and vastest part of the range occupies Middle Asia, Kazakhstan and adjacent territories. In the west, the southern

borders of the distributional area of corsac fox includes the Cis-Caucasian steppes on the south. Beginning on the Caspian coast at Makhachkala, it passes along the foothills to Khasav'yurt, farther to Groznyi and Mozdok, and then, approximately to Stavropol' and from there, embraces the Egorlyk basin, and passes on to the lower Western Manych and to the lower Don [rivers].

278 Along the Don, which constitutes the western border, it rises approximately to 39° N. Lat. (somewhat north of Volgograd)⁵. Thence, the line of the border, following the left bank of the Volga, reaches northward almost to the Samarsk bend, and then ascending somewhat more to the north and to the east and becoming the northern border of the range, it encloses the extreme southern regions of the eastern half of the Tatar Republic (Bugul'minsk, Bavlinsk, approximately at 54° 30' N. Lat.) and adjoining—Bashkiriya. Farther, it passes along the outliers of the Bashkirian steppes and along the Obshchii Syrt it turns sharply to the south to the southern end of the Urals.

Rounding the southern spurs of the Ural mountains along the right bank of the Ural [river], the border on the eastern slope of the range goes northward and passes through Verkhnaural'sk. Thence, going eastward through Troitsk, Shadrinsk, Tyumen', Taru, Ishim, Vengerovo, Barabinsk, Omsk and Lake Chany, the boundary line passes through the bend of the river at Kamen' on Ob'. Following the left bank of the [Ob'] river, it descends to Barnaul, rounds the Altai from the west and along the northern slope of the Zaisan depression, exits into China.

In Middle Asia and Kazakhstan, the range occupies all the level expanses, i.e. corsac fox is absent in Tarbagatai, Dzhungarskii Alatau, in the entire Tien Shan (occurs in the Karatau) and Pamir-Alai and

277 ⁵There is not sufficient exact information about the normal occurrence of corsac fox to the west of the Don. Therefore there is no basis at present to assign the western border of the range along the "eastern part of the Dnepr-Don interfluvium (Pidoplichko, 1951). At the same time, it is probable that some centuries
278 ago, when no cultivation was present in the southern European part of the Soviet Union and people were very scarce, the corsac fox lived somewhat farther west than now; probably it lived normally in the Priazov steppes. However, positive information on this is absent.

It is not excluded that there were intrusions farther to the west as far as Zaporozhsk district and western Priazov. However, intrusions to Zaporozhsk district were extremely rare (Sharleman' [Charlemagne], 1937). There is no basis for believing that corsac fox normally lives and is even sufficiently common (at Korsak-Mogila; Sharleman' [Charlemagne], 1948).

Kopet-Dag. It is found in the level parts of the right bank of the upper Amu-Dar'ya in Tadzhikistan, but it is, apparently, absent in the Fergana valley. From Turkmeniya, where the mountain range (Kopet-Dag) forms no obstacle, the range passes to Afghanistan and Iran, and from eastern Kazakhstan, through the Dzhungarsk Vorota [Gate] and Zaisan depression, into Dzhungariya.

Another section inhabited by corsac fox is found in our country in southern Trans-Baikaliya. This region represents the northern outlier of the Manchurian and Mongolian part of the range. In the adjacent USSR, the range is separated from the already-described western part. The Trans-Baikal section of the range is very small and, in its turn, is divided into two parts. The first includes only the steppes along the Argun' and Onon, and the Aginsk steppe (the area lying to the west of the lower course of the Onon). The second section is still smaller and occupies the steppes along the Selenga and Dzhida in western Trans-Baikaliya.

The northern border of the main range of corsac fox cannot be considered sufficiently defined. Beside the insufficient study of the corresponding territories, the reason for this is that corsac fox is characterized by more or less regular seasonal, and also irregular, migrations. Moreover, through the force of confluence of various ecological conditions, considerable fluctuations exist at places in its numbers, especially at the borders of the range. Finally, the corsac fox under harvest very easily yields to extermination, and slowly restores its numbers. Therefore, in individual years or periods it may, firstly, shift somewhat northward the northern border of its reproductive area or, secondly, there may occur locally quite long transgressions by stray individuals.

At the same time, due primarily to limited information about this species, it is essentially impossible to firmly delimit breeding territory, and territory of migration. The outlined northern border is, to a considerable degree, determined by more or less regular, if nonetheless rare, migrations, and the true limit of the breeding area lies, apparently, somewhat southward. Thus, in southern Tatar Republic, the corsac fox occurs only as a transient (migrating), and the actual [northern] limit between the Volga and Ural apparently lies at the latitude of the Samarsk bend (about 53°). The same thing applies to the extreme northern points where corsac fox is encountered between the Don and Volga. In exactly the same way, the outlined southern and southwestern border in the Cis-Caucasus is, to a

considerable extent determined by migrations. The area of normal occurrence here is restricted (or, until recently was restricted) to the semideserts to the north of the Terek; in the west it did not reach Stavropol'.

Long migrations are known for the corsac fox from the steppes in the southern Ural foothills to Zilair and in Shadrinsk region (at 56°), from the Privolga steppes westward to Hel'govk (about 50 km to the north of Nogaisk on the shore of Berdyansk gulf), and to Pavlograd (east of Dnepropetrovsk). Within the range, there are sections where the corsac fox is absent (Ulutau, Kazakh upland) or they occur as transients (southern Pribalkhash) (see section on "Biology").

Geographic Range outside the Soviet Union

This occupies the steppe part of northeastern China, in all events Barga (expanse between the Argun' and Great Khingans), and probably the Manchurian plains in the Nonn' and Sungari basins; Inner Mongolia; the entire Mongolian Republic, except the taiga districts of the Kentei mountains, the wooded and mountainous districts of the Khangai [mountains], and the Prikosogol'sk district*; Dzhungariya and Kashgariya; Afghanistan (probably only northern regions); and, apparently, northeastern Iran.

280 The limits of the distribution of the corsac fox in southern Central Asia is not known—it is possible that it extends to the ranges that delimit Tibetan Plateau on the north (see section on "Geographic Variation").

Therefore, as a whole, the range consists of two vast areas, western and eastern (central-Asiatic), with a narrow "isthmus" uniting them in the area of the Dzhungarsk Gate and Zaisan depression.

In the Pleistocene, corsac fox was widely distributed in Middle and, apparently, Western Europe and it still lived in the Crimea in the Holocene⁶ (V.H.).

*Area around Hobsogol Lake—Sci. Ed.

⁶Geographic distribution of the corsac fox according to Dinnik, 1914; Ognev, 1931; Shergin and Frenkel', 1936; Sharleman', 1937, 1948; Heptner and Formozov, 1941; Heptner et al., 1950, V.A. Popov and Lukin, 1950; Shvarts, Pavlinin and Danilov, 1951; Pidoplichko, 1951; Kirikov, 1952; Yanushevich and Blagoveshchenskii, 1952; Afanas'ev, Bazhanov et al., 1953; Bannikov, 1954; Vereshchagin, 1958; Sludskii, 1959 and a series of other sources and on unpublished material of V.G. Heptner.



279 Fig. 108. Species range of corsac fox, *Vulpes corsac* L. V.G. Heptner.

Geographic Variation

The geographic variation is quite evidently manifested, although, apparently less than is sometimes considered (Ognev, 1935).

Within the limits of the USSR, one may differentiate the following subspecies.

1. Kazakhstan corsac fox, *V. corsac* Linnaeus, 1768 (synonym *kalmykorum*).

Relatively large form, with fluffy and dense winter fur of above described color, without admixture of reddish tones in winter fur.

Greatest length of skull 103–111 mm, basal length 96–105 mm, zygomatic width 59–68 mm, greatest skull width 37–42 mm, skull height in the region of tympanic bullae 42.6–44 mm, length of upper tooth row 48–55 mm (less than 10 individuals; Ognev, 1931).

Northern part of range of the species, to Cis-Altai steppes. Distributional limits in the south are not established—apparently, it does not extend farther than the latitude of the northern end of the Aral Sea.

Not outside the USSR.

2. Turkmenian corsac fox, *V. c. turcmunica* Ognev, 1935.

Considerably smaller than the preceding (smallest form of the species), with shorter, coarser winter fur, of dirty-grayish color and reddish tones.

There are no data on body measurements.

Skull measurements of Turkmenian corsac fox (14 males and females; V.G. Heptner) are as follows (Table 30).

Inhabits the southern part of the species range—plains of Middle Asia and Kazakhstan, probably, south of the parallel on the Aral Sea's northern end. The boundary with respect to the preceding form is not elucidated—apparently, there is a wide zone of transition between each other.

Outside our borders—in northern Afghanistan and northeastern Iran.

281 The corsac fox of the Volga-Ural steppes and right bank of the Volga apparently has some characteristics of transitional character between the normal form and *turcmunica*. They are described as *kalmykorum*, and their furs are considered as a particular Astrakhan type.

Table 30. Skull measurements of Turkmenian corsac fox (in mm)

Data	Minimum	Maximum	Average
Total length of skull	102.2	114.0	105.8
Condylbasal length	98.4	110.3	103.0
Length of nasal bone along midline	31.7	36.3	33.9
Zygomatic width	57.5	65.3	60.4
Greatest width of cranium	40.7	44.1	42.5
Height in region of tympanic bullae	39.3	43.2	41.6
Length of molar tooth row	38.3	42.5	40.2
Interorbital width	18.4	23.0	20.7

3. Trans-Baikal corsac fox, *V. c. scorodumovi* Dorogostaiskii, 1935 (synonym *nigra*).

There are no data on body measurements.

Skull dimensions of animals from southern Trans-Baikaliya, are as follows (Dorogostaiskii, 1935) (Table 31).

Table 31. Skull measurements of Trans-Baikal corsac fox (in mm)

Data	Males (41 spec.)			Females (37 spec.)		
	Minimum	Maximum	Average	Minimum	Maximum	Average
Greatest length	110.9	124.0	117.0	110.2	119.6	114.6
Condylbasal length	106.0	118.2	113.5	106.0	117.0	110.5
Zygomatic width	63.0	71.1	66.9	63.0	68.8	65.2
Width above canines	18.4	21.5	19.9	18.0	21.5	19.6
Maximum width of cranium	42.0	46.1	44.2	41.4	47.7	43.5
Length of nasal bone	34.0	43.0	38.0	35.0	40.4	37.0
Height in region of tympanic bullae	41.2	45.7	43.7	41.5	45.0	43.1

Found in Trans-Baikaliya.

Outside the USSR, in the Mongolian People's Republic and northeastern China.

To this form, by priority the name *nigra* Kastschenko, 1912 should be assigned; it is based on a skin (without skull) without accurate locality reference, but which apparently originates from Trans-Baikaliya or the contiguous part of the Mongolian Republic. However, this name is hardly acceptable, since the author describes an ordinary melanic, and, due to the defective skin, he is not even sure that it is assignable to this species.

* * *

Separate forms of the corsac fox have not been described from that part of the range lying outside our territory. One may suppose that there, except perhaps in Kashgariya, the same subspecies live which are found in our country.

In the western literature, there is a widely distributed idea (see, e.g., Ellerman and Morrison-Scott, 1951) that *V. eckloni*, described by Przheval'skii (1883) from northern Tibet, constitutes a subspecies of *V. corsac*. This idea is mistaken—*V. eckloni* is a synonym of *V. ferrilata*. The error is probably based on the fact that in

earlier works (in part, as indicated), Przheval'skii called this species the corsac fox (V.H.).

Biology

Population. In the steppes of the Pri-Black and Pri-Azov Seas, corsac fox became extinct, apparently, only in the 18th–19th centuries. The cause for this was believed to be the ploughing of the virgin steppes (Pidoplichko, 1951; Topachevskii, 1956), but, apparently, its extinction took place under the influence of other factors—climatic deterioration (it became less continental) and
282 others. Reduction in numbers of the corsac fox also may have been influenced by the extermination of the steppe marmot [*Marmota bobac*], the burrows of which it occupies particularly eagerly, and by massive reproduction of the red fox in cultivated fields, representing not only its competitors but also its enemies.

At the beginning of the current century, corsac fox was not rare in the Don steppes, in Ergeni [hills] and in the Astrakhan semideserts and south of the latitude of Volgograd (Artsibashev, 1859; Dinnik, 1914; Kirikov, 1959). In recent years, its population even increased, and in Ergeni the animal is now common.

In the Cis-Caucasus, this carnivore is common in the region of the Kumo-Manychsk canal and in the Kum-Terek interfluvium. During this century, in the latter region, its population was subjected to significant changes. Thus, in the beginning of this century, in the northern Caucasus, it was communicated (Dinnik, 1914) that: "Previously, in all these very poorly settled places, corsac foxes lived in great numbers, but with settlement of the steppes and their ploughing, these animals began to greatly decrease in numbers; in many places they even became completely extinct". In 1924–1925, corsac foxes again became numerous in the northeastern Cis-Caucasus. A single hunter caught 15–30 animals in one season (Ognev, 1931; Heptner and Formozov, 1941). By 1931, the population of this carnivore was again strongly reduced. There were relatively many corsac foxes in the Cis-Caucasus in 1951 (Vereshchagin, 1959).

East of the Volga on the Obshchii Syrt and adjacent regions northward to the upper Bol'shoi and Malyi Irgiz rivers, the corsac fox periodically appears common, since its skins are obtained by the hundreds (N. Severtsov, 1861; Zarudnyi, 1897; Bazhanov, 1930; A.A. Sludskii). It is very rarely found in the steppes of Bashkiriya,

penetrating in occasional years to the Beloretsk region and southern Tatarsiya (Popov and Lukin, 1949; Shvarts et al., 1951). At the southern end of the Ural mountains, the corsac fox becomes more common, for example, in Orenburg district, along the border with Kazakhstan. In the Volga-Ural interfluvium, the corsac fox is again frequent and, for example, in the Ural'sk district in different years up to 5,500 individuals are caught in a season, while in Gur'evsk district—up to 1,700. To the south, on the Mangyshlak Peninsula and Ustyurt Plateau, it is common (up to 500 spec. caught per season). It is also common in Mugodzhary.

In western Siberia, the corsac fox appears in various years in the northern forest-steppe zone and even on the edge of taiga forests, but here, its numbers are extremely low. In the southern half of the forest-steppe zone (Barabinsk and Kulundinsk steppes), the corsac fox is rare and not a permanent occupant. In the southern part of the steppe zone of western Siberia (Chelyabinsk, Kustanaisk, Severo-Kazakhstansk, and Pavlodarsk districts and Altai territory), the carnivore being described was common in the last two decades and in some places, it was abundant. In separate years, in each of these districts, from 1000 to 3000 skins were obtained.

The abundance of corsac foxes in typical steppes may be judged by the number caught by hunters. In years with high populations of corsac fox, in central Kazakhstan, hunters catch 20–50 and more animals in a season. In 1947, in Tselinogradsk district, 37 burrows of corsac fox were found in an area of 30 km², and of these 8 had litters, in 8 burrows there had been, apparently, litters, and 9 were inhabited by single animals. In 1948, in this same region, 34 burrows were found, of which only 4 had litters (Chirkova, 1952). It is also numerous in the semideserts of central Kazakhstan (Tselinogradsk and Karagandinsk districts), and also in the Pri-Irtysh steppe (Semipalatinsk district). In some years, in central Kazakhstan, up to 4,500 corsac skins were obtained in a season. In the semidesert, the corsac fox periodically becomes very abundant. Thus, near the Kulanutmes river from July 29 to August 5, 1951, 27 burrows of this animal were found in an area of 1,000 hectares, of which 7 had litters in spring (A.A. Sludskii). In years of massive reproduction, some hunters capture up to 100–120 animals in one season. The corsac fox is abundant from time to time in the Pri-Aral'sk Karakum, common, especially in winter, in Betpak-Dala, occurs in the Pri-Chuisk Muyunkum and in northern Pri-Balkhash'.

In the sandy deserts south and east of Betpak-Dala-Muyunkum, Taukum and Sary-Ishikotrau the corsac fox, as a rule, does not live permanently, but comes from the north only in certain severe winters. This animal is extremely rare in the north and west of the sandy desert of Kyzylkum (Bogdanov, 1882). In the Amu-Dar'ya delta, it is rare (Salikhbaev, 1950). In Kara-Kalpakiya, from 1956 to 1959, only 21 to 76 skins were prepared annually. In the Syr-Dar'ya valley, on the clayey plain Dar'yalyktakyr lying to its north, and in the sands of the Pri-Aral'sk Karakum, the corsac fox is not especially rare, as in the clayey sections of the Ustyurt. There also, on sands, for example Asmantai, they are scarce. In the Ustyurt and in the northern Pri-Caspian, corsac foxes in autumn and winter time are concentrated on the seashore and near the abandoned summer camps and villages, where they feed on refuse and rodents.

In Turkmeniya, it is "very common" in many regions (Radde and Walter, 1889). Thus, it is common on the southern border of the Karakum and in the Badkhyz (Heptner, 1956). At the same time, in the Krasnovodsk region, this carnivore is scarce (Vinogradov, 1952). In the 1924/25 season in Turkmeniya, 11,522 skins were tanned and in 1925/26—7,174 skins (Kogan, 1931). From 1948 to 1959, the number of corsac foxes caught here ranged from 694 (1948) to 2,298 (1956) per year. At the present time, in the majority of places in Turkmeniya, except remote sections of the sands, the corsac fox is common (Sapozhenkov, 1960; V.G. Heptner). In Tadzhikistan, corsac fox is rare in the flat southern and southwestern regions. In the period from 1951 to 1959, only 11 (1952) to 63 (1959) skins were tanned per year. As mentioned above, corsac fox is absent in montane Tadzhikistan.

In Uzbekistan, the corsac fox occupies in all of the plains and foothill desert and semidesert sections, and is common in some places. In the 1924/25 season, 8,039 skins were prepared in the republic and in 1925/26—5,442 (Kogan, 1931). In recent years, the number of animals everywhere decreased (Ishunin and Lustin, 1959), probably in connection with the intensive development of new lands, but in a series of districts, it is common at the present time. Thus, from 1956 to 1959, in Kashkadar'insk district, from 580 to 1,244 corsac foxes were caught per year, in Bukhara—from 395 to 546, in Samarkand—from 288 to 474, and in the Tashkent—from 208 to 336. In the Fergana valley, they are obtained singly from 1956—

1959, 1–12 skins. The corsac fox is rare in Korezmsk (16–88 skins per year) and Surkhandar'insk districts (68–94 skins per year).

In Kirghiziya, in the 60's of the previous century (N.A. Severtsov, 1873) the corsac fox was common not only in the Chuisk and Talassk valleys, but also in high mountane regions (Susamyrsk Plateau, Dzhumgal, the Lake Sonkul' depression, on the Aksai and in the lower reaches of the Chirchik, Arys, and Keles rivers). However this information is doubtful. In the last decade, the corsac fox was not found permanently in any place in Kirghiziya (Kuznetsov, 1948). In the severe winters of 1948/1949 and 1950/1951, these animals appeared in the Chuisk valley and the foothills adjacent to it, and became fairly common there. In 1956–1959, Kirghiziya yielded 131–137 skins of this animal.

In southeastern Kazakhstan (southern Pri-Balkhash', Chu-Iliisk mountains, foothill regions of the Zailiisk and Dzhungarsk Alatau, Alakul'sk depression), the corsac fox was extremely rare and was caught singly until the 50's of the present century. In many regions, it was completely unknown. Starting from 1951, populations of the animals here started to grow rapidly and in recent years in Alma-Atinsk and Dzhambul'sk districts, up to 1000–1300 skins began to be taken annually.

In southern Pri-Baikal the corsac is "very rare" (Selenga valley; Fetisov, 1949) and does not appear every year (Surmach, 1957). In southeastern Trans-Baikaliya in the middle of the last century, the corsac fox was very common in the montane steppes (Maak, 1859). "Along the Argun' and Onon they are a multitude" (Cherkasov, 1884). Later, in connection with the ploughing of the steppes, numbers of these animals strongly decreased in eastern Siberia and in the 20's of the present century only 341 skins were tanned in 1925/26 and in 1926/27, 333 skins. In the 30's, the number of corsac foxes here again grew, and up to 1,400 corsac began to be caught in a year (Podarevskii, 1936). In the last two decades, the number of the corsac foxes in Trans-Baikaliya has again decreased (see "Population").

Therefore, within the boundaries of USSR, the corsac fox is most numerous in dry steppes and semideserts (central Kazakhstan). In deserts of the northern and southern types (southern Kazakhstan, Turkmeniya, Uzbekistan) this carnivore is less numerous, but in places it is common and even abundant.

In the 18th century, in the territory of contemporary Kazakhstan, corsac was much more numerous than now. At that time, Kazakhs sent from 40 to 50 thousand skins every year to Orenburg and Troitsk fortresses (Rychkov, 1762). "Innumera copia" (innumerable multitude)—thus was described the number of corsac foxes in Kazakhstan at the end of the 18th century and beginning of the 19th by G. Fisher (1814). Later, as a result of intensive harvest and especially ploughing of the steppes, the populations of corsac fox started to decrease. They declined especially strongly after 1954 in connection with massive ploughing of virgin lands.

The corsac fox is numerous in the Mongolian People's Republic. In individual years, up to 18 (1928) and even 24 thousand skins (1931) were obtained there. About 90% of this quantity was obtained from the eastern plain-steppe and semidesert regions (Bannikov, 1954). In the province of Xinjiang (China), in Iran and in Afghanistan, the corsac fox is rare. In northern Afghanistan, however, it is quite common (V.G. Heptner).

Habitat. In the Pri-Azov the corsac fox is restricted to the weakly undulating plains of the watersheds which are occupied by Pri-Black Sea herbaceous-fescue-feather grass and fescue-feather grass steppes, as in the southern *chernozem*. Here are innumerable ravines and gullies, at the heads of which the soils are salinized and have semidesert vegetation, covered mainly by fescue, meadow grass (*Poa bulbosa*) and desert-steppe shrubs: prostrate summer cypress (*Kochia prostrata*) and various species of sagebrush; also thickets of steppe shrubs—blackthorn (*Prunus stepposa*), spiraea, Russian peashrub (*Caragana frutex*) and others. These steppes were formerly inhabited by bobac marmots [*M. bobac*]. At the present time all of these steppes are almost completely destroyed, in connection with which the corsac fox lives there on the *solonchak* [areas of saline soil] near the seashore (Korsak-mogila) [Corsac-grave], in elevated areas; and along southern slopes of gullies as well as in pastures.

In the western half of the Cis-Caucasus, this carnivore lives in steppes very similar to those already described, while in the Pri-Caspian and the lower Volga, the corsac fox inhabits sagebrush-turf-grass steppes and semishrub sagebrush and Russian thistle desert (southern semidesert), and is also encountered on compacted sands (Nogaïsk steppe). In the Volga-Ural interfluvium, the corsac fox inhabits the steppes, semideserts and deserts, but it is more common

in hilly semideserts with a low and scattered stands of grass; along the middle course of the Ural river, on the Obschii Syrt and on the upper Chagan river, it lives in the hilly steppes (Zarudnyi, 1894) and chiefly inhabits the slopes of hills scattered across the level feather grass-sagebrush semidesert (Kuznetsov, 1928). In the Volga-Ural sands, it is rarely met with and, apparently, is not permanent.

During years of increase, it inhabits even the forest-steppe of western Siberia beyond the Ural mountains, with its flat relief where the low and narrow ridges ("crests") 2 to 4 m high, rarely 6 to 10 m, alternate with the depressions occupied by lakes, rush-covered floodlands, small birch forest—*kolka* ["pins"]—and *solonchak*. In the forest-steppe, the corsac fox mainly inhabits *solonetz* [alkaline] soils around large salt lakes with poor vegetation and occasionally the crests if they contain significant sections of virgin soil with low fescue steppe. It hunts mainly around water
285 bodies with open shores, on *solonchak*, in depressions and along crests where little snow occurs in winter. It flees into *kolka* and rush-covered floodlands only during periods of ice crusts, where it searches for white hares [*Lepus timidus*] and willow ptarmigan [*Lagopus lagopus*] caught in snares (Sludskii, 1930).

South of the forest-steppe, from the left bank of the Volga and to the Ob' [river], the corsac fox lives in herbaceous-fescue-feather grass steppes on ordinary and southern *chernozem* (Kulundinsk steppe), and also in turf-grass dry steppes lying more to the south. In the typical steppes, the corsac fox settles in the burrows of marmot and ground squirrels, located on the gentle slopes of elevated areas not far from the edges of *solonchak*, and in summer it hunts mainly in places with scarce vegetation. There, where the steppes are ploughed, the corsac fox survives only in pastures and near bodies of waters; it is often obliged to live near villages.

In winter, the corsac fox chooses places where the snow is blown clear by wind or is light, but it also appears in thickets of reeds near bodies of water. Thus, in the very snowy winter of 1940/41, in Severo-Kazakhstansk district, corsac foxes were found in considerable numbers on the steep slopes of the great Lake Chagla depression, where there was little snow and it could prey on voles and mice. Driven by hunger, the corsac foxes were captured in cut reeds growing around the lake, under which there was little snow and where they hunted the water voles [*Arvicola terrestris*] which were very numerous there.

In Kazakhstan, the corsac fox is especially numerous in desert steppes between the Ural and Embi, along the Turgai and south of Lake Kurgal'dzhin and the Nura river. There is undulating or hilly relief with narrow river valleys and quite expansive depressions with fresh and salt lakes. In these regions, the corsac fox occupies gentle sides of valleys and slopes and is usually absent in *melkosopochnik* [region of small mounds or hills], occurring only around the base of the *sopok* [mounds]. Thus, southeast of Lake Kurgal'dzhin, near the Kulanutmes river, burrows were distributed on the upper parts of the slope—the watershed between the Kulanutmes and a deep narrow valley. From the river to the summit of the slope was 2–3 km. The gentle declination of the slope was occupied by fescue-feather grass steppe with 30–50% of the soil covered with vegetation. In the upper part of the slope, old burrows of marmots and ground squirrels were encountered. Corsac foxes also used them as dens.

The building of a burrow by corsac foxes on elevated areas (excluding *melkosopochnik*) is explained by the high flooding of the steppe rivers; the water level of which rises 10–14 m. Building their burrows in the higher part of knolls, the corsac fox in summer hunts along their slopes, and rarely appears at the bottom of ravines, or at the river or lake, but it usually avoids entering hilly country. In autumn and the beginning of winter, in the northern semidesert (Lake Kurgal'dzhin), it restricts itself to flat areas, overgrown with sagebrush and Russian thistle (B.D. Abaturvov).

After abundant snowfall, when the depth of snow cover in areas with tall vegetation reaches 20 to 40 cm, and it becomes more densely packed, while in areas with low vegetation cover (in sagebrush, sagebrush-fescue and sagebrush-saltbush [*Atriplex cana*] associations), snow cover is shallow; the corsac fox prefers such sections with little snow or places with very packed snow. There, the winter burrows are also found, located along more elevated areas.

Farther to the south, the corsac fox lives in true deserts of the northern type, inhabiting the entire Betpak-Dala. In summer, it is rarely encountered here. For nine years, on an itinerary extending for a total of ten thousand kilometers, only four burrows with litters were found. In Betpak-Dala, the corsac fox settles on the summits of knolls covered with small sagebrush and usually 200–300 m from a spring with water. In the last decade, corsac foxes became

common in the foothills of Zailiisk Alatau, where they inhabit hilly
286 clayey deserts and semideserts, not long ago inhabited by yellow
ground squirrels [*Spermophilus fulvus*], in the burrows of which
the foxes construct their lairs. Here, the corsac fox finds favorable
conditions, since food is abundant, snow in winter is not deep, and
is often trampled down by numerous cattle herds grazing there.

The corsac fox inhabits the ephemeral deserts of Turkmeniya,
Tadzhikistan and Uzbekistan. Along the lower Amu-Dar'ya, it oc-
cupies the old valleys and deltas, but everywhere it is quite rare
(Kostin, 1956). In clayey deserts of southwestern Turkmeniya, it is
met with everywhere, and is not rare in compact sands. In south-
eastern Turkmeniya, the corsac fox is found in the clayey deserts
and semideserts and along the edges of compact sands. It is com-
mon in the southern margins of the Karakum; it often remains near
wells. There, its burrows are found on the slopes of sandy hillocks
inhabited by the great gerbil [*Rhombomys opimus*]. In Tadzhikistan
and Uzbekistan, it inhabits desert areas on the plain and in the

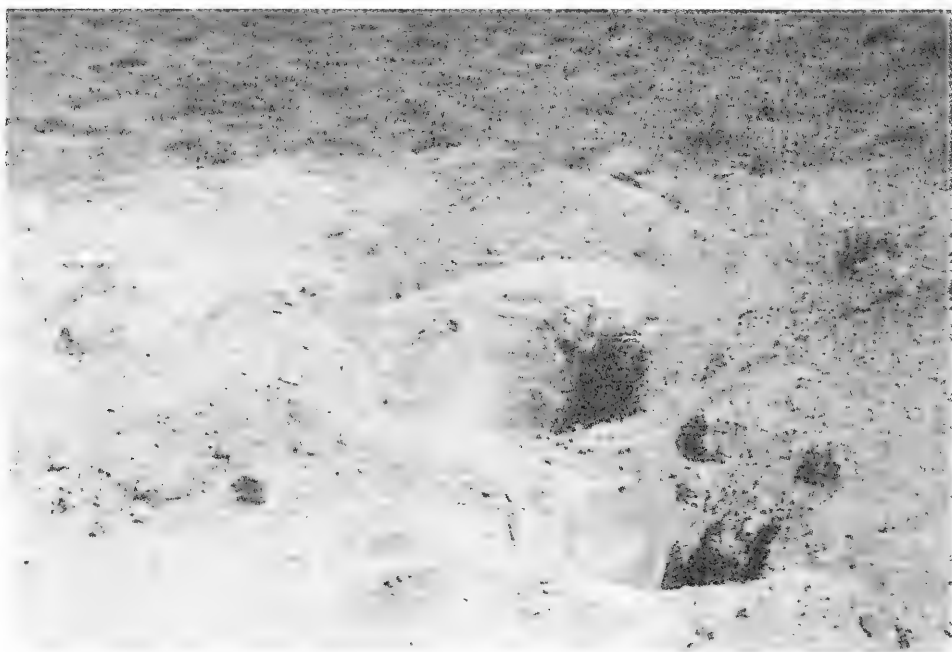


Fig. 109. Burrow of corsac fox. Betpak-Dala desert. Kazakhstan. 16 June,
1956. Photograph by A.A. Sludskii.

foothills, old river valleys and the small sandy massifs. It is absent in *tugai* [riparian] forests (Chernyshev, 1958).

In southern Pri-Baikal and southeastern Trans-Baikal, the corsac fox inhabits hilly steppes, well-supplied with mounds having flat summits 50–100 m high which are irregularly scattered or extending as low chains. The slopes of the *sopok* are gentle, and pass gradually into wide depressions. In places on the hills and in the steppe, there are rocky exposures and outcrops. Among the rocks and near them, forbs and shrubs grow vigorously which are rarely encountered in the ravines. On large areas, the grassy steppes stretch over sandy and sandy-gravelly soil, mainly wild calla* cattail and wild rye-cattail steppes. In the steppes, the grassy and sagebrush areas form a complicated mosaic. The region is characterized by low temperatures in winter (to -50°C), shallow snow cover—on average only 10 cm—and permafrost located at a depth of 2.0–2.6 m. In Trans-Baikaliya, the corsac fox inhabit the slopes of valleys well-supplied with tarbagan [*Marmota sibirica*] burrows which they occupy for their shelters.

287 In the MNR [Mongolian People's Republic], the typical habitat is more or less level or slightly undulating dry steppes with small, shallow valleys with a cover of feather grass, feather grass-bistort or grass-Russian thistle. This carnivore is rarer in herbaceous steppes of the northern type, and still more rarely encountered in montane steppes, whence it penetrates along the river valleys. It avoids mountainous relief with cliffs and rock slides as well as true shrub deserts.

Accordingly, throughout the entire range of the corsac fox, the main habitats are the semideserts and the dry steppes resembling them. In grassy steppes, it chooses areas with scattered, low grass and shrub cover. Everywhere, it avoids dense thickets and prefers the plains. The corsac fox is absent in areas with loose snow cover more than 15 cm in depth, but there, where snow is compact or blown away by wind, it may exist even when the average depth is 30 to 50 cm deep.

Food. The corsac fox is a carnivore, adapted to hunt small and moderate-size lagomorphs and rodents, including young marmots and hares. In summer time, small birds, reptiles and insects also occupy a considerable place in its diet. In distinction from other

*The Russian word "zmeevik" is used for 5 different genera, including *Polygonum*, *Calla* and "tyrsa" is defined as *Typha*—Sci. Ed.

species of the family of our fauna, it rarely feeds on plant food. In case of insufficient prey, it eats carrion and refuse, often poorly-digestible.

In connection with the wide distribution of the corsac fox, its food list varies, but everywhere rodents predominate. At the northern limits of the range, in the forest-steppe of western Siberia (Barabinsk steppe), this carnivore in summer preys on narrow-skulled voles [*Microtus gregalis*] or *Alticola strelzovi* and sagebrush voles [*Lagurus lagurus*]; rarely does its prey extend to water voles [*Arvicola terrestris*], red-cheeked ground squirrels [*Spermophilus erythrogenys*], great jerboas [*Allactaga jaculus**], common hamsters [*Cricetus cricetus*], Dzhungarian hamsters [*Cricetulus sungorus*], larks, charadriiformes and ducks. In winter, it preys mainly on mouse-like rodents, but occasionally attacks white hares, willow ptarmigan, gray partridge [*Perdix perdix*], black larks [*Melanocorypha yeltoniensis*] and snow buntings [*Plectrophenax nivalis*]. Near villages, it feeds on carrion and refuse; several individuals gathering around a large carcass (Sludskii, 1930). In the steppes of Kazakhstan, a basic role in the food is also played by mouse-like rodents (99.4%), among them the sagebrush vole (37.9%). Apparently, this rodent is more often eaten, since of the numerous remains of unidentified voles found in the feces a significant part
 288 also (48.5%) belong to it (Table 32). In this region, birds are also important in the food of corsac fox (35.5%), apparently wounded ones.

In the steppes in winter, the corsac fox feeds on mouse-like rodents, but when they are scarce or not obtainable, it turns to other species of prey. Thus, in the heavy snow winter of 1940/41, in Severo-Kazakhstansk district, at Lake Chagla during a time of frozen snow-crust, corsac foxes hunted water voles in cut reeds, digging up their runways in the thawed soil, and also gray partridge which spent the night in shrubbery near the lake. These carnivores also remained near cattle burial grounds and villages, where they fed on carrion and refuse.

In 890 feces of corsac fox collected in May–June 1947 and 1948, near Tselinograd, remains of rodents were found in 95.4% of all samples investigated, corresponding to: birds in 17.0%, insects in 22.1%, reptiles in 0.8%, plants remains in 2.1% and indigestible refuse (rags, ropes, etc.) in 0.4% (A.F. Chirkova). Among mouse-like rodents, the main mass consisted of sagebrush voles, while

*Now called *A. major*—Sci. Ed.

287 **Table 32. Results of feces analysis of corsac fox inhabiting the Kazakhstan steppes (Severno-Kazakhstansk district, Sovetsk region, near Lake Chagla, July, 1947; from burrow with litters; 169 samples; frequency of occurrence in %)**

Food type	%
<i>Mammals</i>	99.4
<i>Rodents</i>	99.4
Various voles	99.3
Including:	
Sagebrush vole [<i>Lagurus lagurus</i>]	37.9
Common vole [<i>Microtus arvalis</i>]	0.6
Narrow-skulled vole [<i>Microtus gregalis</i>]	7.7
Root vole [<i>Microtus oeconomus</i>]	4.2
Unidentified voles	48.5
House mouse [<i>Mus musculus</i>]	0.6
<i>Birds</i>	35.5
Ducks	14.8
<i>Insects</i>	7.1
Beetles	7.1

common, root and narrow-skulled voles, mole-vole [*Ellobius*] and wood mice [*Apodemus*] were rarer. The remains of white hare, red-cheeked ground squirrel, jerboa, shrews—brown-toothed [*Sorex*] and white-toothed [*Crocidura*—were found on isolated occasions.

In the semideserts and dry steppes of central Kazakhstan in the spring—summer period, corsac foxes hunted mainly intensively reproducing sagebrush voles (encountered in 96.1% to 98.7% of all samples examined). Other voles, rats, hares, steppe pika [*Ochotona pusilla*], hamsters [*Cricetus*] and dwarf hamsters [*Cricetulus*] were rarely met with in the feces and clearly played no notable role in its diet. At the same time, the role of ground squirrels and jerboas here was increased. Thus, e.g. at Karsakpai, the remains of yellow ground squirrels were found in 13.3% of the samples, while in the Atbasarsk region of Tselinograd district, in 7.1%, although there this ground squirrel lives at the northern limit of its range. In the latter region, the remains of intermediate ground squirrels [*Spermophilus intermedius*]* were found in 7.2% of the excrements, while those of jerboas—in 14.2% (Kh. Kydyrbaev). In the Basaga region, jerboas were found in 10.7% of the samples (see Table 33).

*Synonym, *S. brevicauda*; usually considered a subspecies of *S. erythrogenys*—Sci. Ed.

289 Table 33. Results of feces analysis of corsac fox inhabiting the semidesert of central Kazakhstan (in % of number of samples)

Region, season and year, number of samples Food type	Northern semidesert near Kulantumes river		Southern semidesert—Karsakpai, Kazakhstan upland, Basaga ⁷		
	Summer, 1950 417	Summer, 1951 1518	Spring, 1950 45	Summer, 1953 103	Summer, 1954 132
<i>Mammals</i>	99.8	99.4	100.0	100.0	100.0
Lagomorphs and rodents	99.8	99.3	100.0	100.0	100.0
Steppe pika [<i>Ochotona pusilla</i>]	—	0.1	2.2	4.0	3.8
Mongolian pika [<i>O. pallasii</i>]	—	—	—	2.0	1.5
White hare [<i>Lepus timidus</i>]	0.2	0.4	—	—	—
Yellow ground squirrel	—	—	13.3	—	—
[<i>Spermophilus fulvus</i>]					
Ground squirrel [<i>S. intermedius</i>]	0.5	0.1	—	5.8	—
Little ground squirrel	—	—	2.2	—	—
[<i>S. pygmaeus</i>]					
Ground squirrel (unidentified)	0.5	0.2	—	13.8	—
Steppe mouse [<i>Sicista subtilis</i>]	—	0.3	—	—	—
Great jerboa [<i>Allactaga jaculus</i>]	—	0.5	—	—	—
Small five-toed jerboa	—	—	2.2	—	—
[<i>A. elater</i>]					
Thick-tailed three-toed jerboa	—	—	—	2.0	—
[<i>Stylodipus telum</i>]					
Jerboas (unidentified)	1.0	4.3	—	10.7	0.8
Common hamster	—	0.1	—	—	—
[<i>Cricetus cricetus</i>]					
Eversmann's hamster	0.7	0.1	—	—	—
[<i>Cricetulus eversmanni</i>]					
Gray hamster [<i>C. migratorius</i>]	—	—	—	3.0	—
Sagebrush vole	98.7	96.6	75.6	96.1	97.0
[<i>Lagurus lagurus</i>]					
Mole-vole [<i>Ellobius</i>]	2.9	0.1	—	—	—
Water vole [<i>Arvicola terrestris</i>]	—	0.1	—	—	—
Common vole	0.2	—	8.9	—	—
[<i>Microtus arvalis</i>]					
Narrow-skulled vole	—	—	—	9.7	12.1
[<i>M. gregalis</i>]					
House mouse [<i>Mus musculus</i>]	—	0.7	—	—	—
Striped field-mouse	0.2	—	—	—	—
[<i>Apodemus agrarius</i>]					
Wood-mouse [<i>A. sylvaticus</i>]	—	0.4	—	—	—
Small rodents (unidentified)	0.1	0.3	—	—	—
Carnivores	0.5	0.5	—	—	—

(contd.)

(Table 33—contd.)

Food type	Region, season and year, number of samples	Northern semidesert near Kulantumes river		Southern semidesert— Karsakpai, Kazakhstan upland, Basaga ⁷		
		Summer, 1950	Summer, 1951	Spring, 1950	Summer, 1953	Summer, 1954
		417	1518	45	103	132
Weasel [<i>Mustela nivalis</i>]		0.5	0.3	—	—	—
Corsac fox (wool)		—	0.2	—	—	—
<i>Birds</i>		18.7	16.7	—	5.8	6.8
Ruddy Shelduck		0.2	—	—	—	—
Ducks (unidentified)		1.2	—	—	—	—
Large birds		4.6	0.7	—	—	—
White-winged lark		2.4	0.9	—	—	—
Small birds (unidentified)		10.6	16.0	—	—	—
Duck eggs		0.2	0.1	—	—	—
<i>Reptiles</i>		1.7	3.1	—	2.0	1.5
Sand lizard		0.1	1.3	—	—	—
Lizards (unidentified)		0.5	1.1	—	2.0	1.5
Patterned rat-snake		—	0.1	—	—	—
Mamushi		—	0.1	—	—	—
Snakes (unidentified)		0.2	0.5	—	—	—
<i>Insects</i>		22.0	17.4	—	15.8	4.5
Locust		—	1.1	—	—	—
Beetles		22.0	16.3	—	—	—
Eggs of praying mantis		—	0.1	—	—	—
<i>Plants (grasses)</i>		0.2	0.1	—	—	—
<i>Carriion</i>		—	0.1	—	—	—

⁷According to the data of G. Shubin.

In places where the tarbagan marmot is still numerous, it apparently plays a considerable role in the summer diet of corsac foxes, since in Trans-Baikaliya, corsac foxes catch young bobaks and feed on the dead bodies of adult animals (see below).

In the semidesert, the role of reptiles among the corsac fox's food is negligible (1.5–3.1%). The same may be said about insects in years of rodent abundance (see Table 33). In a time of depression of mouse-like rodent populations (1960), in the region of Lake Kurgal'dzhin, the feces of corsac fox consisted, to a considerable degree, of remains of grasshoppers (B.A. Abaturov). Birds have a more basic importance in the food of the corsac fox in semideserts (5.8–18.7% occurrence). In summer, this carnivore almost never eats carrion, but of plants it consumes small quantities of grass leaves.

In winter, with sagebrush voles abundant, and obtainable, the corsac fox continues to hunt this rodent principally, and, for example, in the region of Lake Kurgal'dzhin in the winter of 1959/60, all of its feces consisted entirely of the remains of mouse-like rodents. Moreover, in river floodplains, they successfully attack white hares; hunt black larks hiding in the snow at night from bad weather. Holes of corsac fox were found in early spring which contained shells of bird eggs buried by them in the ground. In the winter of 1960/61 in the region of Lake Kurgal'dzhin, when sagebrush voles were very scarce, corsac foxes restricted themselves to harvested fields and roads. In fields, they hunted harvest mice [*Micromys minutus*], house mice and common voles, and also gathered the seeds of cereal crops. In winter, feces were, mainly, mouse-like rodents, but contained also remains of seeds of corn [maize], oats and barley. The hungry animals dug out from under the snow old boots, soles, rags, ropes and gnawed them (B.A. 290 Abaturon). There, they also picked up small fish discarded by fishermen. In Tselinograd district in the winter of 1940/41, which distinguished itself by its abundant snow and frozen crust, corsac foxes destroyed white and common hares so intensely that their number became considerably reduced. An analogous picture was also observed there in the winter of 1953/54. After a thaw and the formation of a strong ice crust, corsac foxes began to starve and appeared in great numbers in the river floodplains and clearings, where they intensively hunted white hares or remained near villages where they fed on refuse. Feeding of corsac foxes in winter, a time of famine for them, on refuse near populated areas, and even the outskirts of such large cities as Pavlodar and Karaganda, is a common phenomenon.

In deserts of the northern type, extending in Kazakhstan from the northern Pri-Caspian to the Alakul'sk depression, rodents continue to predominate in the summer food of corsac foxes (87.3–100% of all occurrences) (see Tables 34 and 35), but the importance of different species of animals changes greatly. Mouse-like rodents, especially the sagebrush vole [*Lagurus*] stand as secondary* prey. Only in the foothills of the Zailiisk Alatau and in a few other similar places, was the social vole [*Microtus socialis*] encountered in 70.8% of occurrences, and in the foothills of Bulattau (northeastern Betpak-Dala)—in 38.4% of samples studied.

*From context, probably should read "primary"—Sci. Ed.

291 Table 34. Results of feces analysis of corsac fox inhabiting northern type clayey deserts in Kazakhstan (in % of sample number)

Region, year, number of samples Food type	Pri-Caspian lowland, Makat	Foothill, Zailiisk Alatau, Samsy	Alakul' depression, Uch-Aral
	May 1934 798 ⁸	May-June 1954-1955 209 ⁹	April-June, 1954 131 ¹⁰
<i>Mammals</i>	—	99.0	100.0
Lagomorphs and rodents	—	99.0	100.0
Hares [<i>Lepus</i> sp.]*	1.0	—	—
Yellow ground squirrel [<i>S. fulvus</i>]	—	40.2	—
Little ground squirrel [<i>S. pygmaeus</i>]	12.0	—	—
Great jerboa [<i>Allactaga jaculus</i>]	0.6	0.5	—
Earth hare [<i>A. jaculus</i>]**	1.1	—	—
Small five-toed jerboa [<i>A. elater</i>]	—	1.0	—
Fat-tailed jerboa [<i>Pygerymus platyurus</i>]	0.2	—	—
Thick-tailed three-toed jerboa [<i>Stylodipus telum</i>]	4.0	—	—
Jerboas (unidentified)	19.1	—	5.3
Migratory (gray) hamster [<i>Cricetulus migratorius</i>]	—	—	19.1
Eversmann's hamster [<i>C. eversmanni</i>]	1.6	—	—
Tamarisk gerbil [<i>Meriones tamariscinus</i>]	—	11.5	2.3
Mid-day gerbil [<i>M. meridianus</i>]	0.6	—	—
Gerbils (unidentified)	3.5	—	—
Mole-vole [<i>Ellobius</i>]	—	6.0	—
Muskrat [<i>Ondatra zibethicus</i>]	—	—	13.0
Social vole [<i>Microtus socialis</i>]	8.2	70.8	5.3
Root vole [<i>M. oeconomus</i>]	—	—	7.3
Voies (unidentified)	—	—	22.9
House mouse [<i>Mus musculus</i>]	—	6.0	1.5
Mouse-like rodents	22.5	—	29.6
Rodents (unidentified)	7.0	—	—
<i>Carnivores</i>	—	0.5	—
Steppe polecat [<i>Mustela eversmanni</i>]	—	0.5	—
<i>Insectivores</i>	1.5	—	—
Long-eared hedgehog [<i>Hemiechinus auritus</i>]	1.5	—	—

(contd.)

*In the Russian original, *zayats-rusak*, which is the name applied to *L. europaeus*. This is evidently a *lapsus*, and *L. tolai* is meant—Sci. Ed.

**In the Russian original, *zemlyanoi zaichik*, another common name for the great jerboa. Probably a *lapsus*—Sci. Ed.

(Table 34—contd.)

Region, year, number of samples Food type	Pri-Caspian lowland, Makat	Foothill, Zailiisk Alatau, Samsy	Alakul' depression, Uch-Aral
	May 1934 798 ⁸	May-June 1954-1955 209 ⁹	April-June, 1954 131 ¹⁰
<i>Birds</i>	10.5	3.0	3.8
Gray partridge [<i>Perdix perdix</i>]	0.3	—	—
Merlin [<i>Falco columbarius</i>]	0.1	—	—
Kestrel [<i>Falco</i> sp.]	0.1	—	—
Gray lark [<i>Calandrella pispoletta</i>]	0.2	—	—
Passiformes (unidentified)	—	3.0	2.3
<i>Birds</i> (unidentified)	9.8	—	1.5
<i>Reptiles</i>	1.4	0.5	43.5
Lizards	—	0.5	30.5
Snakes	—	—	13.0
<i>Insects</i>	1.6	16.0	—
Locust	—	—	1.5
Mole crickets	—	—	38.9
Beetles	—	16.0	29.7
Insects (unidentified)	—	—	45.0
<i>Plants</i> (grass leaves, seeds of barley and wheat).	1.5	6.0	6.9
<i>Carrion</i> (of sheep, camels)	2.1	—	—

⁸Kolosov (1935).⁹Kh. Kydyrbaev.¹⁰Khusainov (1959).

In the food of desert corsac foxes, jerboas play an important role. In the Pri-Caspian lowlands, they were noted in 25%, while in the clayey-gravelly Betpak-Dala—in 30.2–77.8% of examined samples.

Rodents of medium size occupy second place. In the Pri-Caspian lowland, these are the little ground squirrel [*S. pygmaeus*] (12.0% occurrence), in the northwestern part of the Betpak-Dala—the intermediate ground squirrel [*S. intermedius*] (43.7–61.9% occurrence) and the steppe pika [*O. pusilla*] (53.8% occurrence); lastly, in the foothills of the Zailiisk Alatau—the yellow ground squirrel [*S. fulvus*] (40.2% occurrence) (see Tables 34 and 35). In the southern part of Betpak-Dala, the great gerbil [*R. opimus*] was noted in 92.0% of feces examined, and on the edge of Taukum (southern Pri-Balkhash)—in 40%. In the latter region, jerboas (40%), social voles

292 **Table 35. Results of feces analysis of corsac fox inhabiting desert of the northern type—Betpak-Dala (in % of sample number)**

Food type	Region, year number of samples	Southern (Koktal)	Central (Sorbulak)	Northeastern (Bulattau)	
		June 1955, 112 ¹¹	May 1954, 103	May 1956, 63	May 1951, 13
<i>Mammals</i>		—	100	100	100
Lagomorphs and rodents		—	96.1	87.3	92.3
Steppe pika [<i>Ochotona pusilla</i>]		—	54.4	—	—
Mongolian pika [<i>O. pallasi</i>]		—	—	—	53.8
Tolai hare [<i>Lepus tolai</i>]		4.5	—	—	—
Intermediate ground squirrel [<i>S. intermedius</i>]		11.6	43.7	61.9	7.7
Jerboas (unidentified)		42.0	77.7	30.2	23.0
Migratory (gray) hamster		7.2	1.0	—	—
Great gerbil [<i>R. opimus</i>]		92.0	—	—	—
Voles (unidentified)		—	1.0	1.6	38.4
<i>Carnivores</i>		—	—	—	7.7
Weasel [<i>Mustela nivalis</i>]		—	—	—	7.7
<i>Ungulates</i>		—	2.9	11.1	—
Saiga [<i>Saiga tatarica</i>]		—	2.9	7.9	—
Goitered gazelle [<i>Gazella subgutterosa</i>]		—	—	3.2	—
<i>Insectivores</i>		1.8	1.9	3.2	—
Long-eared hedgehog [<i>Hemiechinus auritus</i>]		1.8	1.9	3.2	—
<i>Birds</i> (passiformes)		2.7	12.6	31.7	7.7
<i>Reptiles</i>		7.1	1.9	15.9	7.7
Lizards		6.2	1.9	7.9	—
Snakes		0.9	—	7.9	7.7
<i>Insects</i>		34.0	19.4	36.5	15.4
Beetles		34.0	19.4	36.5	15.4

(20%) and insects (beetles) (40%) of feces studied are of greatest importance in food of the corsac fox.

292 Near a burrow with a litter (14 May 1952, at the edge of Taukum desert), remains of black-bellied sandgrouse and steppe larks were found, and at a family burrow in the Ili' delta (May 1961), remains of house mice, narrow-skulled voles [*M. gregalis*], muskrats and Semirechensk pheasants were found. The presence of remains of saiga and goitered gazelle in corsac fox feces in

¹¹M.I. Ismagilov.

spring must be attributed to carrion feeding. In some deserts birds, mainly passeriformes, sometimes occupy an essential place for the described predator (up to 31.7% occurrence) (see Table 35). Corsac fox attacks even such large birds as graylag goose [*Anser anser*]. At the end of July 1936, on Lake Telikul', was observed how it concealed itself at midday from adult birds sitting on the shore. It successfully attacked young wild geese and ducks on Barsa-Kel'mes Island (Aral Sea; Sludskii, 1939).

The corsac fox readily feeds on lizards, snakes (eastern snake, chicken and rat snakes) and young steppe [Horsfield's] terrapins especially in years with low numbers of rodents. In the Alakul' depression, in spring and summer 1954, when the number of rodents was low, 43.5% of corsac feces near burrows with litters contained remains of reptiles, mainly lizards (30.5%). Insects are regularly eaten by corsac foxes in the desert and in considerable quantities, but usually do not play an important role in the diet. During insufficiency of rodents, they occupied a prominent place in the nutrition of a corsac fox family in Alakul' depression in 1954 (see Table 34). Mole crickets (38.9% occurrence) and beetles are particularly often eaten. Plant remains are rarely found. Usually, these are grass leaves, and in the foothills of the Zailiisk Alatau, the animals in spring gleaned seeds of wheat and barley remaining on the soil surface after sowing.

293 When it turns cold and the snow falls in the desert and semi-desert zone, the corsac fox is deprived of many foods: rodents entering into winter torpor, migratory birds, reptiles and insects. The remaining voles, pikas and gerbils which retain an active mode of life exhibit reduced surface activity or shift to a subnival mode of life. Therefore, the majority of corsac foxes leave summer habitats and migrate in search of food to the river valleys (Ural, Emba, Syr-Dar'ya, Chu, Ili), and to sand [deserts] (Pri-Aral Karakum, Pri-Chu Muyunkum, Sary-Ishikotrau), and sometimes northward into the dry steppes. In winter both migratory and sedentary animals feed mainly on the remains of saigas and goitered gazelles preyed on by wolves, and on carrion. In searching for carrion and refuse, corsac foxes move at that time nearer to populated places and roadbeds of railway lines. Feeding on the remains of the wolf's prey, corsac foxes become their true commensals. For instance, in the Ural-Kushum interfluvium, in the winter of 1953/54, in December–January, corsac foxes fed mainly on the carcasses of male saigas killed by

wolves. In 10 animals, caught in the Betpak-Dala desert from November 27 to December 21, the remains of saigas were found in 70% of the stomachs. In the middle of December, 1955, in the central part of Betpak-Dala, several corsac foxes were found at each saiga carcass.

Food of the corsac fox in southern (ephemeral) deserts has not been studied. Judging by the faunal composition of these deserts, one may suppose that in summer it feeds there, apparently, on great and red-tailed [Libyan] gerbils, yellow ground squirrel, various species of jerboas and birds, reptiles and insects, and in winter, on gerbils and rarely on jerboas and birds.

In the steppes of southeastern Trans-Baikaliya summer food of the corsac fox consists mainly of rodents (99.2–100% occurrence) (see Table 36). It quite often feeds on tarbagan marmots (18.8–71.0% occurrence) and Daurian pika (29.2 to 62.8% occurrence). Voles and hamsters stand in second place in its food, then birds, and lastly—tolai hare, Daurian ground squirrel, jerboa [*Allactaga sibirica*], insectivorous and carnivorous mammals, and insects. Characteristically, in Trans-Baikaliya, reptiles, which are rare there, are lacking in the food of corsac fox. It more often feeds on plant than, for example, in the steppes of Kazakhstan.

The corsac fox, attacking a tarbagan marmot, causes relatively little harm, except to the young. These rodents do not especially fear corsac foxes and rarely conceal themselves in burrows on their approach. They only interrupt feeding, sit “like a stump”, and call. Not rarely one may observe how an adult tarbagan marmot attacks a corsac fox, jumping out from its burrow or drawing nearer and nearer, and drives it away from the mound. Tarbagan marmots a year old or more, on being kept in a cage with an adult corsac fox, remained alive during the course of several days, notwithstanding that the carnivores were not fed during this time. Under similar conditions, young tarbagan marmots (several months in age) quickly became victims of the corsac foxes (Brom, 1952). Remains of 23 tarbagan marmots, found near and in the burrow of a corsac fox consisted of: juveniles (*mendel*)—4, animals in their second year (*kotel*)—16; and adults—3 (Nasimovich, 1951). It is believed that the corsac fox can kill only young tarbagan marmots, but among the adults, it takes solely dead ones (Nasimovich, 1951; Brom, 1952). Sometimes marmot families with young live next to a corsac fox litter and the carnivores do not touch them.

294 Table 36. Food of corsac foxes in the steppes of southeastern Trans-Baikal based on analysis of samples from contents of their stomachs and feces (in % of sample numbers)

Food type	Season of year, material	Summer			Winter	
		52 stomachs ¹²	feces		38 sto- machs ¹⁴	feces 323 samples
			56 samples ¹²	500 sam- ples ¹³		
<i>Mammals</i>		100.00	100.00	99.4	52.6	—
Lagomorphs and rodents		100.00	100.00	99.2	39.4	94.2
Tolai hare [<i>Lepus tolai</i>]		—	1.5	—	7.9	—
Daurian pika [<i>Ochotona daurica</i>]		32.6	29.2	62.8	—	51.1
Daurian ground squirrel [<i>Spermophilus dauricus</i>]		3.8	7.7	1.0	—	—
Tarbagan marmot [<i>Marmota sibirica</i>]		71.0	60.0	18.8	5.2	50.8
Jumping jerboa [<i>Allactaga sibirica saltator</i>]		1.9	6.1	2.0	2.6	0.3
Daurian [striped] hamster [<i>Cricetulus barabensis</i>]		—	—	—	10.5	2.5
Dzhungarian hamster [<i>Phodopus sungorus</i>]		7.7	1.5	—	2.6	2.8
Hamsters (unidentified)		7.7	12.3	0.6	—	6.8
Trans-Baikal tsokor [<i>Myospalax</i>]		—	—	—	2.6	—
Michnoi vole [<i>Microtus michnoi</i>]		—	—	—	5.2	—
Narrow-skulled vole [<i>M. gregalis</i>]		7.7	9.2	—	2.6	3.7
Brandt's vole [<i>M. brandti</i>]		9.6	6.1	—	7.9	5.6
Voles (unidentified)		1.9	12.3	13.0	21.0	12.7
House mouse [<i>Mus musculus</i>]		—	1.5	—	—	0.3
Murids (unidentified)		5.8	3.0	16.8	—	—
Chiroptera		—	1.5	—	—	—
<i>Insectivores</i>		1.9	3.0	—	7.9	1.2
Daurian hedgehog [<i>Mesechinus dauuricus</i>]		—	3.0	—	2.6	1.2
Red-toothed shrews [<i>Sorex</i> sp.]		1.9	—	—	5.2	—
<i>Carnivores</i>		7.7	1.5	0.2	5.2	1.2
Steppe polecat [<i>Mustela eversmanni</i>]		—	—	—	5.2	—
Solongoi [<i>M. altaica</i>]		—	—	0.2	—	—
Corsac fox		7.7	1.5	—	—	1.2
<i>Ungulates</i>		3.8	15.6	0.2	2.6	3.4
Mongolian gazelle [<i>Procapra gutturosa</i>]		—	15.6	—	—	3.4

(contd.)

(Table 36—contd.)

Food type \ Season of year, material	Summer			Winter	
	52 stomachs ¹²	feces		38 sto- machs ¹⁴	feces 323 samples
		56 samples ¹²	500 sam- ples ¹³		
Roe deer [<i>Capreolus capreolus</i>]	—	—	—	2.6	—
Carrion (domestic animals)	3.8	27.6	0.2	23.7	32.7
Birds	7.7	15.3	33.4	26.3	13.0
Daurian partridge [<i>Perdix daurica</i>]	—	—	—	7.9	—
Mongolian lark [<i>Melanocorypha mongolica</i>]	—	—	—	2.6	—
Small birds	—	—	—	10.5	—
Insects	55.7	27.6	9.8	2.6	3.4
Plants	32.7	37.0	1.8	10.5	30.6
Refuse (pieces of twine, rags, dressed skin, etc.)	—	3.0	—	59.9	9.3
Soil, pebbles	63.4	63.0	—	—	13.3

¹²Brom (1952).¹³Nasimovich (1951).¹⁴Skalon (1936).

The negligible percent occurrence of mouse-like rodents, especially Brandt's vole, in stomachs and feces, is probably explained by the small numbers of voles present in the years when the materials were collected. Occurrences in summer feces of Mongolian gazelle and domestic animals may be interpreted as the remains of wolf meals and carrion. Observations exist of corsac foxes catching fish in the summer of 1944, in the dried-up lakes on the floodplain of the Argun' river (Brom, 1952). In half of all the examined stomachs of corsac foxes and in 25% of their feces are found insects, though as separate individuals. Of plant food, fruits of sweetbrier were found.

In Trans-Baikaliya, the winter ration of the corsac fox hardly differs from summer (see Table 36). Only in individual years, during low rodent populations, feeding on carrion and various refuse grows. In winter, a great quantity of tarbagan marmots are found in stomachs and feces of corsac foxes (up to 51.1% occurrence). Apparently, at this time, corsac foxes feed on carcasses of tarbagan marmots, which die in summer burrows and were preserved there by the cold (Cherkasov, 1884; Brom, 1952). Through tracks, it was observed how the corsac foxes dig out from the snow the

entrances to abandoned marmot burrows and enter them. Frequent
 295 feeding by corsac foxes on carcasses of marmots indicates that in
 these regions, intensive epizootics occur among rodents. Occur-
 rences of remains of Mongolian gazelle and roe deer are explained
 in that the corsac fox in this region, as in Kazakhstan, feeds on the
 remains of wolf prey and on carrion.

In the Mongolian People's Republic, Brandt's vole constitutes
 the food base of the corsac fox in summer and winter, while other
 rodents (gerbillines and hamsters) are of secondary importance.
 Thus, on May 24, in the Choibalsan region in a burrow with a litter,
 91 carcasses of mammals were found, of which 80 were Brandt's
 voles. In a burrow found on July 9 near Ulan-Tsirik, among 46
 animal carcasses, 45 belonged to this same vole (Kucheruk and
 Dunaeva, 1948). In Kentei aimak*, in two corsac fox burrows
 excavated in May and June, remains of Mongolian gazelles, Cen-
 tral-Asiatic [upland] buzzard [*Buteo hemilasius*] and horned lark
 [*Eremophila alpestris*] were found, and in feces, the remains of
 Brandt's vole and birds. Brandt's vole, within the limits of its range,
 constitutes the main food of the corsac fox (Skalon, 1949). In the
 stomachs of corsac foxes caught in spring and the beginning of
 summer, Brandt's vole, Daurian pika, quite a few orthopterous
 insects and bones of small fish were present. The corsac fox eats
selitryanka fruits (*Nitraria schoberi*). More or fewer numbers of
 remains of orthopterans may also be found in winter feces of the
 corsac fox. Hunters believe that grasshoppers are a winter tidbit
 for this carnivore; therefore, they already prepare them early in
 autumn and use them in quantity as bait in traps. In southwestern
 Khangai, in winter, corsac foxes also feed mainly on Brandt's
 voles, but also eat insects. Corsac foxes, especially young, feed on
 orthopterans in other seasons also; with an abundance of locust, the
 stomachs of the carnivores are literally stuffed with these insects
 even during times of mass reproduction in Brandt's voles (P.P.
 Tarasov).

In the Mongolian Republic in winter, corsac foxes often feed on
 carrion and refuse and closely approach populated places, appear-
 ing even at the outskirts of Ulan-Bator [Ulaanbaator]. Sometimes,
 corsac foxes become commensals with respect to diurnal raptorial
 birds—upland buzzard (*Buteo hemilasius*) and saker falcon (*Falco*
cherrug milvipes), many of which winter in the northern part of

*Province—Sci. Ed.

the Mongolian Republic. Corsac foxes gather remains of their prey, and at this time the stomachs of the animals become filled with hind limbs, intestines and heads of voles; i.e., all the parts which buzzards and falcons leave rather than eat (P.P. Tarasov). Feeding mainly on rodents, corsac foxes in the steppes and semideserts are concentrated in places with an abundance of sagebrush voles or Brandt's voles, migrating there from the neighboring regions (Nekipelov, 1935; Brom, 1952; Peshkov, 1954). They also gather in regions where epizootics are spreading among rodents, or where mass mortality has occurred among wild ungulates and cattle during a prolonged period of continuous snow cover [dzhut].

With insufficiency of mouse-like and other rodents, or when they are unavailable, corsac foxes suffer from hunger, markedly lose weight and even die. In search of prey, they undertake migrations of considerable distances (see later). Corsac foxes may remain without food for 7–15 days and maintain their activity. During the course of such a period, they sometimes do not leave the burrow, particularly if a trap is set at its entrance.

Corsac foxes held in captivity in autumn consumed the following amounts of food: males—from 120 to 480 g, averaging 218–347 g (various individuals); females—from 100 to 395 g, averaging 245–259 g (two individuals; Brom, 1952). In Betpak-Dala, in the animals caught in December in the early morning hours or at night, the weight of the contents of a fully filled stomach was equal to 100–130 g. Taking into consideration that the corsac fox hunts twice daily—at dawn and at night—its natural daily ration in the wild is approximately equal to 200–260 g, comparable to the contents in captivity. In order to be sated, it is sufficient to it to eat one pika (200 g) or about five voles.

- 296 In Betpak-Dala, in individual stomachs, the following foods were found: female, on May 17—intermediate ground squirrel (adult), darkling beetles; subadult male, on October 8—gray lark [*Calandrella pispoletta*], mole crickets (7); female, on October 18—red-tailed gerbil [*Meriones erythrouros*], eastern sand snake; female, on November 27—saiga meat and fat, social vole [*Microtus socialis*] (2); female on December 21—saiga meat, red-tailed gerbil, lizard [*Phrynocephalus* sp.]. In Trans-Baikaliya, in individual stomachs of corsac foxes caught in January were found: 1) Michnoi vole [*Microtus michnoi*], Daurian hamster [*Cricetulus barabensis*], Daurian partridge, 10 pieces of linen rags, 2) Daurian hedgehog

[*Mesechinus dauuricus*], Daurian partridge, a piece of shoe, 3) gray [brown] rat [*Rattus norvegicus*], a vole, a hamster, a shrew, and grass leaves (Skalon, 1936).

With abundant prey, many carcasses may be brought into or near the burrow by corsac foxes (see above). In the foothills of the Zailiisk Alatau, carcasses of yellow ground squirrels (*S. fulvus*) were found at the burrows, but rarely other food. On 29 May 1955, at one burrow, 8 carcasses of yellow ground squirrels plus 8 heads and 4 tails, a tail of a small five-toed jerboa [*A. elater*] and the body of a lark, were found; at a second burrow, on 9 July 1955, 15 carcasses and 8 heads of ground squirrels were found (Kh. Kydyrbaev). Such accumulations of carcasses are usually known as "reserve", but actually are the remains of collected food. Sometimes, in periods of famine, corsac foxes eat the carcasses of their fellows (Brom, 1952).

In the desert, the corsac fox is more often encountered near wells and springs with water, but they are not attracted to them by the water itself, but by the abundance of food. Even P.S. Pallas (1811) noticed that the corsac fox rarely drinks and can remain for a long time without it. "In captivity, and when fed meat, corsac foxes can do well without water, and if it is offered to them in the cage, they are completely unattracted to it" (Nasimovich, 1951).

Home range. The dimensions of denning and hunting areas of the corsac fox are little known. In the Pri-Caspian lowland, when corsac fox was common, one litter occupied an area of 30–40 km². Burrows were unevenly distributed around the territory, occupying the more elevated parts (Kolosov, 1935). In the steppes of Tselinograd district, one burrow occupied an area of 0.8 km², and 1.9–3.7 km² for one litter (Chirkova, 1952). In the same district, near the Kulanutmes river (semidesert), in 1951, when corsac foxes were common, there were 27 burrows in an area of 10 km², 7 of which had litters. In the following year, after a sharp decrease in the corsac fox population, in the same place in an area of 2.7 km², only one of 13 burrows found was inhabited; one corsac fox lived in it. In the Kurgal'dzhin Lake region, in the winter of 1959/60, at the end of February in an area of 1 km² 5 inhabited burrows of corsac foxes were found, and 6 of these animals also were observed there (B.D. Abaturov).

In southeastern Trans-Baikaliya, in the first half of August, the young of one litter lived within a radius of 300 m of the den burrow

and spent the daytime in one or another tarbagan marmot burrows. In this area, the corsac pups played, ran from one marmot mound to another and entered the occupied and unoccupied tarbagan burrows. In these same steppes, corsac foxes bringing prey to the pups were observed at a distance of 6 km from their den burrow (Brom et al., 1948). In the latter case, the hunting region of the corsac fox family must have occupied about 113 km². In winter, in 1948, in Trans-Baikaliya one corsac fox occupied 3 km² (Brom, 1952).

Burrows and shelters. The corsac fox is a relatively weak animal, has many enemies, and therefore, in open landscapes, it must hide in burrows and other shelters. The corsac fox uses burrows also as protection from low or very high temperatures. The corsac fox is a poor burrower, and cannot dig in hard ground. Therefore, it adapted to living in foreign burrows: of marmots—bobak [*M. bobak*] and tarbagan [*M. sibirica*] and large ground squirrels—yellow [*S. fulvus*]—reddish [*S. major*] and red-cheeked [*S. erythrogenys*]. It easily enters the openings into marmot burrows, but has to widen those of ground squirrels in order to dwell there. Rarely, it occupies abandoned burrows of red foxes and badgers; only in soft sand or clay-alkaline ground does it dig itself simple and usually shallow burrows. Thus, in the Barabinsk forest-steppe, living places of this animal are simple in construction. They have 1 to 4 entrances not more than 1 meter deep. In the center of passages or at their end, the den chamber is built, which has no bedding throughout the whole year. In the forest-steppes, the corsac fox adopts for its own shelter the burrows of red-cheeked ground squirrels, widening them, or inhabits old burrows of red foxes and badgers. There, it digs itself only a shallow shelter with a short passage, known by hunters as “*dnevki*” [day rest]. They use these only in summer for resting and for hiding in case of danger. In warm times of year, it usually rests by lying under a shrub, or in grass. In winter a corsac fox, caught by a snowstorm in the steppe, far from burrows, lies in a hollow dug into a snowdrift and allows itself to be drifted over. It rarely hides in straw- or haystacks. During snowfalls, it does not leave the burrow for 2–3 days (Sludskii, 1930).

In the steppes of Severo-Kazakhstansk district, the corsac fox is adapted to the burrows of ground squirrels or marmots. The burrow depth here is 40–150 cm, being explained by the ground water level and deep winter snow cover. In the Sovetsk region, 1.5

km from Lake Chagla, in sagebrush-grass steppe, the den burrow of the corsac fox has 2 exits, the general length of the passage is 4 m with side branches of 70 and 200 cm. Maximum depth of hiding passages is 40 cm. Dimensions of den chamber are 30 × 40 cm; in it bedding is absent. On the surface between entrances, the animals clear a small area, known by hunters as a "*tochok*".

In the semidesert of central Kazakhstan near the Kulanutmes river, the majority of 38 burrows found were situated on the summits of ridges, part on gentle slopes and a small number in the bottoms of valleys. Entrances to burrows are often oriented toward the north-northeast or northwest, and only in individual cases toward the southeast and other directions. Entrance diameter varies from 20 to 30 cm, with the average equal to 22 cm. Thirty burrows (79%) had only one entrance, 2 had two entrances, 4 had three and only 2 had 4. The majority of burrows are simple, and have only one passage ending in a chamber. Complex burrows, with several entrances and side-burrows, were rarely met with. Passage length ranged from 140 to 450 cm, on average equaling 240 cm (of 12 burrows). Greatest depth of litter in passages varied from 55 to 115



297 Fig. 110. Corsac fox burrow under rock outcrop in semidesert at Kulanutme
298 river, central Kazakhstan. 27 July 1951. Photograph by E.I. Strautman.

cm, the average equaling 79 cm (of 11 burrows). The upper portion of the burrow passages went through soft loamy soil, the chamber was always located in very hard gypsum of a clay layer, which could be cut only by an axe. All burrows were constructed in old ground squirrel shelters. Chambers had dimensions of 40 × 30 cm. In none of these was bedding found at the beginning of August.

Soil thrown out by the animals from the burrows does not form a high mound of elongated form in front of it as is observed at red fox burrows, but is scattered evenly around the entrance. Thanks to this characteristic, to detect a corsac burrow it is more difficult than that of a red fox. Around the den burrow occur many feces of both adults, and especially, young. Moreover, some meters from the entrance, in specially made pits are 2–4 “latrines.” Near and to the side of many burrows there are 1–4 “*tochok*”, on which the young pups played. In three cases, the living places were distributed in groups of 3 to 4 burrows each, and each one of the shelters was a distance of 40 to 500 m from the other; they were connected to each other by trails. Such groups of burrows belong to one family. In the Kurgal’dzhin Lake region, in the river valley, all corsac fox burrows also were located in groups on elevations which are not submerged by snow melt-water. In other sections there, although single burrows were encountered, most areas were uninhabited (B.D. Abaturov).

At 100 to 300 m from the den burrow, temporary burrows (“*dnevki*”) were sometimes met, with a passage length from 50 to 120 cm containing no chambers. At the beginning of August, in 12 burrows and 4 “*dnevki*”, 7 young animals were found; in one burrow—2, while in the remaining—singles. Usually, 70 to 80% of the burrows are uninhabited.

In semidesert, the corsac fox utilizes burrows throughout the whole winter. The entrance into the burrow is always cleared of snow, which forms a small hillock. At the beginning of winter, often there are several entrances cleared of snow, but by midwinter the corsac fox cleans only one entrance of snow. A burrow dug in the Kurgal’dzhin Lake region had, in the middle of winter, a length of 2.5 m and depth of 1.5 m. To a distance of 40 cm, the passage was covered by hoar-frost, but beyond that thawed soil was found (B.D. Abaturov).

In Betpak-Dala, corsac fox builds more complicated burrows than in the steppe and semidesert, in relation to shallow snow cover



298 Fig. 111. Old den burrow of corsac fox with 23 exits. Edge of Karakum desert near Tashkepri on the Murgab, Turkmeniya, 23 April 1962. Photograph by A.A. Sludskii.

in winter, high air temperature in summer, and loose ground which is easily excavated. Here, burrows are located on gentle slopes of ridges or on level plateaus. Of 6 burrows, one had 3 entrances, two—6, the remainder—8, 10 and 14 entrances. A family with 5 young lived in a burrow with three entrances on level ground among peanut bushes. A second burrow was dug on a gentle south slope covered by sagebrush and peanuts near a small *solonchak* 300 m from a spring with water. It possessed 14 entrances, distributed over an area 7 m in diameter. The passages led to a den chamber located at a depth of 120 cm. At a distance of 70 m was located another burrow with 6 entrances and an area strongly beaten down by the playing of the young pups. The family of these animals used two burrows simultaneously, in that in the burrow with 14 entrances the parental pair lived, and in the burrow with six entrances—8 young.

A group of three burrows was located on a slightly undulating clayey plain covered with sagebrush. The first possessed 18

entrances and was uninhabited. Forty meter from it was located a second burrow with 6 entrances used only periodically. At 20 m from the latter, a third, with 10 entrances, was inhabited. In it at a depth of 125 cm was located a den chamber, in which was caught an adult female and 3 young animals. Near the burrow there were two cleared "*tochok*". In the passages of the burrow were found carcasses of five intermediate ground squirrels, badly decomposed and with masses of fly maggots, remains of a small jerboa [*A. elater*], larks and desert wheatears [*Oenanthe deserti*]. At the entrance to the burrow, little excrement was found, but the remains of three intermediate ground squirrels, two eastern sand snakes and some larks and desert wheatears were found. In a small side-burrow, 12 scorpions were found. A complicated burrow with 6 entrances was found in a *solonchak* on the edge of the Taukum sands.

Burrows of corsac fox in the northern Caucasus are also situated in groups (Dinnik, 1914). In this region, with sandy subsoil, it is easy for the animals to dig burrows, and they are built very widely. Each complex burrow with many deep-lying passages occupied an area having a diameter of perhaps about 40 to 60 m in diameter. Sometimes, such burrows were located near each other. These complex burrows received the name "corsac city" from hunters. They believed that they were inhabited by many animals that lived in a sort of colony. If such vast burrows actually existed, they were inhabited, as a rule, by one family consisting of a pair of adult animals and their litter.

On Barsa-Kel'mes Island in the Aral Sea, corsac foxes lived in the burrows of yellow ground squirrels, suitably widened by them. The length of their passages reached 4 m and were situated at a depth of 1–1.5 m (Sludskii, 1939).

In the steppes of southeastern Trans-Baikaliya and the northern part of the Mongolian Republic, the corsac fox lives almost exclusively in the abandoned burrows of tarbagan marmots (Cherkasov, 1884; Nekipelov, 1935, 1952; Brom et al., 1948; Nasimovich, 1951; P.P. Tarasov). The corsac fox does not widen the tarbagan's burrows. Corsac foxes often visit occupied burrows of tarbagans (Brom et al., 1948).

In southeastern Trans-Baikaliya, in the course of six warm months, the average caught out of each uninhabited [tarbagan] burrow was: 0.6 corsac fox in 1947, 0.2 in 1948, 0.1 in 1949

(Nekipelov, 1952). In the Mongolian Republic, the corsac fox sometimes lives in burrows of the Daurian ground squirrel [*Spermophilus dauricus*] after widening them. Five burrows found here had from 1 to 5 entrances. A denning burrow had one entrance and a den chamber of 40 × 30 cm, without bedding (Skalon, 1949).

300 Therefore, in clayey steppes and semideserts, burrows of the corsac fox are relatively simple and usually not deep. In snowless deserts, especially in areas with soft ground, burrows occur that are especially complex, and den chambers are situated deep. Den chambers are also located deep in southeastern Trans-Baikaliya and the Mongolian Republic, where winters are very severe and snow is scant. The corsac fox does not strew grass in the den chamber. Everywhere, corsac foxes build their burrows on plains and on gentle slopes of ridges and hills. Burrows do not occur in ravines, on steep slopes or among thickets.

Many symbionts use burrows of the corsac fox. In inhabited burrows, parasites (fleas) and nidicoles (flies, beetles and others)* are numerous. Scorpions were also found. The shelduck (*Tadorna tadorna*) and ruddy shelduck (*Tadorna ferruginea*) nest in abandon burrows. Renard's viper (*Vipera ursini*) and other reptiles were also encountered there.

Daily activity and behavior. The corsac fox was previously considered an exclusively nocturnal animal. However, recent observations have shown that it mainly leads a crepuscular mode of life, and diurnal activity occurs, especially during the period the young are being fed, when food is insufficient, and in times of winter frosts.

Due to its relatively imperfect thermoregulation, the corsac fox is obliged to use burrows more often than other foxes to reduce its activity. At times of strong freezes and wind, it remains in the burrow for longer than does the red fox. In the Barabinsk steppe, during strong snowstorms, corsac foxes did not leave the burrows for 2–3 days. Adapting to cold, the whole litter often lives in the burrow in winter. Because of this, 2 to 5 animals are successfully dug out simultaneously from one burrow (Sludskii, 1930). Even in severe freezes, the corsac foxes, being hungry must remain long outside the burrow searching for prey. On calm frosty days, the animal may be observed lying on the snow near the entrance to a burrow, while the snow beneath it does not thaw.

*Nest inhabitants—Sci. Ed.



300- Fig. 112. Corsac fox burrow near Imam-Baba. Edge of Karakum, Murgab.
301 22 April 1962. Photograph by A.A. Sludskii.

301 The corsac fox inhabits semideserts and deserts, where air temperature in summer rises to 40°C and even to 50°C, and the soil surface becomes heated to 75°C and more. The corsac fox escapes from such high temperatures in burrows and in the warm season, it chiefly leads a crepuscular mode of life.

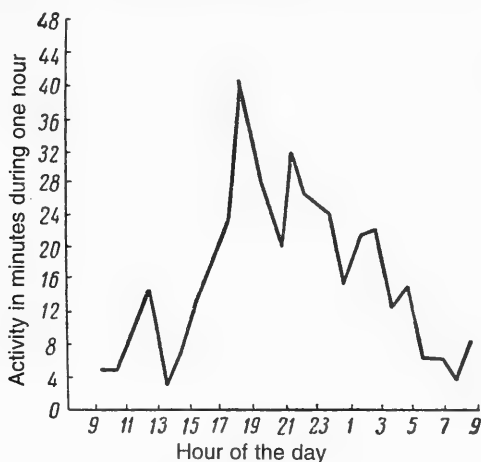
The corsac fox is a carnivore, capable of capturing food only in those places where there are no dense thickets (in summer) or deep snow cover (in winter). The corsac fox is not adapted to movement on snow. In the animals from Betpak-Dala, the length of the forelimb from the chest to the ground ranges, in males, from 17 to 23 cm (average—19.0 cm; 6 specimens) and, in females, from 16 to 19 cm (average—17.3 cm; 9 specimens), while in the Karagan red foxes obtained from the same region, corresponding values are 26.3 and 24.0 cm, respectively. In spite of low weight (2.0–2.5 kg), the corsac fox has a great weight loading on the supporting surface of the foot—61 g/cm² for male animals from Trans-Baikaliya (Nasimovich, 1951). In animals from Betpak-Dala (males), it is from 68.3 to 80.0, or an average of 75.2 g/cm² (4 specimens), and in females it is from 43.6 to 74.0—an average of 54.4 g/cm² (9 specimens). In Karagan red fox, this weight loading is 62 g/cm² in males and 60 g/cm² in females, and in red foxes from heavy snow regions, it is less: in Lapland red fox—27–30 g/cm² (Nasimovich, 302 1948) and in Pechora red fox—28 g/cm² (Teplova and Teplov, 1947). Thanks to the great weight loading and relatively short limbs, the corsac fox deeply sinks into loose snow, and with snow cover depth of 15–20 cm, it moves with great difficulty. At that time, the corsac fox stays in burrows or uses trails and tracks of other animals and humans. In distinction from the red fox, the corsac fox does not have a “mouse-leap”—a unique jump on rodents found under the layer of loose snow. Therefore, with deep snow cover, corsac foxes seek out areas where the snow is blown off or compacted by wind, and they also are restricted to places of winter grazing by large herds of saigas and domestic livestock. In obtaining food from under the snow while winter grazing, these ungulates dig up and trampling it, help the corsac fox to move and to catch rodents (Skalon, 1952; A.A. Sludskii). In the presence of deep snow cover, hard-crusts or ice-covered ground, the animals suffer from hunger and leave that region.

In places with tall grass cover (meadow grass) as, for instance, in Badkhyz (southern Turkmeniya), corsac foxes constantly use the

numerous trails beaten by goitered gazelle and kulan (V.G. Heptner). In winter, corsac foxes were observed at carrion during the day, and on windless sunny days, lying on the snow near a burrow (Sludskii, 1930; B.D. Abaturon). In Betpak-Dala, corsac foxes were met with in December around 10–11 in the morning, and during the afternoon, when they approached domiciles to feed on refuse. At that time, they were also active after dark. The same thing is known for southeastern Trans-Baikaliya and Mongolian People's Republic (Brom et al., 1948; Skalon, 1949, N.V. Nekipelov). In the northern part of the Mongolian Republic, the corsac fox in winter begins hunting at the end of the day, before evening and scurries about searching for food the entire first half of the night; it again hunts early in the morning, and very rarely during daytime.

In summer, corsac foxes are also active not only at twilight and at night, but often hunt during the day, especially when they are feeding young (Nasimovich, 1951). In captivity, at air temperature from 3° to 10°C, corsac foxes were active at 1900, 2300 and 0200 hours [Fig. 113]. With reduction of air temperature from 25 to 0°C, activity of the corsac fox decreased threefold (Kalabukhov and Poluzadova, 1946; Kalabukhov, 1950).

Young animals, 1.5–2 months of age, assume a more diurnal mode of life. Thus, in Betpak-Dala, from 11 to 27 May, a litter of 8 pups might be observed on the surface already at 5 in the morning. Until 9 am, the corsac pups played near the burrow entrance,



301 Fig. 113. Daily cycle of activity of corsac fox in an experiment at 3–10°C (after Kalabukhov, 1950).

moving not more than 5 meters away. When it became hot, they hid in the burrow and by 11 am only individual animals remained on the surface, but in the course of the whole day 1 to 2 corsac pups usually were lying near the burrow, sometimes changing places. At the end of the day, the corsac pups came out from the burrows more frequently and remained on the surface for a longer time. By 20:00 hours, the whole litter was already inside the burrow. Coming out of the burrow, the corsac pups looked around for a long time, moved slowly and often scratched; apparently, they were greatly disturbed by fleas. At sunset, they cautiously began to play. When threatened by danger, they broke off playing and stretching their necks, endeavored to see what had frightened them. When afraid, the pups barked, making a sound which may be given as "vyau-vyau". After quieting down, the corsac pups again returned to play which continued until the approach of full darkness. But even later, at 11, 12 and 1 at night, when the burrow was illuminated, the whole litter could be seen near it.

When coming out of burrows, the corsac fox at first thrusts out its head only, then shows itself to the shoulder, and only after being sure that it is quiet all around, does it come out on the surface. After coming out, the animal stretches itself several times, looks around, and then sits down, or sometimes lies down, near the burrow, continuing to observe its surroundings. Sensing danger, it sits and watches closely, slightly nodding its head. If the alarm is shown to be not false, it begins "barking" in that direction, continuing, however, to sit in its place. After quieting down, with the approach of twilight, it sets out on the hunt and already at 21:00 hours, the animal could be observed beating back and forth along the road for jerboas.

303 Both in summer and in winter the corsac fox, lying near the burrow entrance, does not respond to a human approaching it before a distance of 30 to 50 meters; after that, it runs aside and does not run into the burrow. When followed, it runs to a neighboring burrow, and remains motionless. Thus, even injured animals behave in the same manner, but when escaping from a wolf or eagle, the corsac fox enters the first available burrow, even if inhabited by marmots.

It is interesting that the corsac fox has the ability to remain motionless, feigning death. The animal is sometimes found thus in an excavated burrow. It lies completely without movement, relaxed

and with its eyes closed. Taken up in the hands, it remains in this state, completely lifeless. But, if it is put on the ground, it opens its eyes, jumps up and runs away. (Similar behavior is known for red foxes, jackals, striped hyaenas, ratels, raccoon dogs and especially opossums.)

The corsac fox is somewhat timid and cautious. It permits humans to approach as near as 10 meters, and then runs off for 100–200 m and remains motionless. It also permits a car as close as 5–6 meters. It is caught in traps more easily than the red fox. With abundant food, for example, at a time of massive death of ungulates from starvation, it sometimes remains with red foxes and even dogs near carrion at cattle burial grounds and dumps (Sludskii, 1930).

In summer, corsac foxes hunt alone: the animal slowly walks against the wind and on smelling or seeing prey, conceals itself by pressing to the ground and running from one cover to another. Not far from the intended victim, it jumps up and overtakes it in a few springs. Rarely, it runs at a slow gait, and startling its prey, for example, sagebrush vole, pursues its prey, and overtaking it, endeavors to pin it with its front feet. Where jerboas are numerous, it watches for them by remaining motionless behind bushes along roads or paths, where these rodents run, at the approach of twilight or at sunrise. On the ground, it searches for nests and preying on nesting birds, eats the nestlings and eggs. It catches goslings when their parents lead them to the steppe to feed, and ducklings at the time the adults lead them from the nest to water or transfer them from one lake to another. The corsac fox hunts lizards by jumping on little shrubs under which they are hidden, and endeavoring to roust them into the open.

In winter, it also searches for food singly. In the literature, there is some information stating that corsac foxes sometimes hunt in pairs or even in small packs. Actually, they gather as several individuals around large carrion, but approach it singly, following the tracks or trail trampled by other animals.

In the search for scarce winter prey, the animal goes at a trot, stopping and sniffing. Scenting or hearing the squeak of an animal under the snow, it quickly digs the snow trying to catch the rodent. With snow cover deeper than 10–15 cm, or when it is compact or covered with a hard crust, the hunt of the corsac fox is usually unsuccessful.

Corsac fox possesses a good sense of smell. One can successfully follow by tracks on the snow how it turned at a right angle to its path and 20–30 m to the side dug out from under the snow an old sheep leg, horse hoof or leather scrap (Brom, 1952). The corsac fox preys on willow ptarmigan and gray partridge night-roosting in the snow, black larks and snow buntings, and watch for white hares on their trails. In breaks in the reeds, the soil buried under the snow is not frozen, and it catches water voles by excavating their burrows.

Corsac fox tames well, and can live in captivity for a long time.

Seasonal migrations and transgression. The approach of cold, the entrance into hibernation of rodents, the torpor of reptiles and insects, the migrations of a series of birds and the falling of snow force the corsac fox, in late autumn or the beginning of winter, to migrate to the south, but sometimes also in other directions. Obtaining winter food, which is rare itself, becomes more difficult if snow cover is deep—more than 15 cm, or forms a hard
304 snow crust or ice-covered ground. Abundance and availability of food depend also on other factors: severe frosts at the beginning of winter when there is still no snow, steppe fires, migration of ungulates, etc. All these phenomena often take place in the forest-steppe, steppe, and some in the northern deserts of Kazakhstan.

In individual winters, the number of corsac foxes in the steppes increases from the tally of animals arriving from the forest-steppe, and with low numbers or difficulties in capturing rodents in the steppe, corsac foxes leave it for the semidesert. In the northern and central parts of its range, including the northern deserts, the seasonal migrations of these animals bear a more or less regular character and take place almost annually. In the beginning of winter, the majority of corsac foxes abandon summer places and search for sections richer in food (Polferov, 1896). In the steppes of northern Kazakhstan, in the heavy snow winter of 1940/41, corsac foxes (and also wolves and red foxes), migrated *en masse* to the southwest to the Turgai river and were encountered in Priishmisk and other regions of Severno-Kazakhstansk district, where they had not been previously observed for many years (I.R. Zenkin). In the winter of 1942/43, in these same places, corsac foxes migrated to the north. One hunter there caught 56 animals in the season, at a time when, in the usual years, only 2–6 animals were caught (E.E. Chernov). In 1947 (in November), intensive emigration to the south of corsac foxes was observed there, connected with the low

number of mouse-like rodents in the places of their summer residence. In the heavy snow winter of 1948/49, massive emigration of corsac foxes was recorded in Kustanai district. The animals went to the south, while from the steppes of Tselinograd district, some migrated to the south and others to the northeast, towards Om'sk and Pavlodar. As a result, corsac fox population decreased by about 40% (K.T. Popov). In 1950/51, in connection with the early formation of snow cover, which was very compact as a result of thawing and refreezing, forming a thick frozen ice-crust, from the middle of December massive emigration to the south was observed from Kustanai, Tselinograd and Karaganda districts.

Such migrations of corsac foxes, having in different years various directions and intensity, depending upon weather and food abundance, were also observed in other parts of the range. By the middle of December, with the formation of a deep snow cover in the semidesert, the population of corsac foxes in Betpak-Dala increases as a result of migration from the north. At that time, their tracks are encountered in great numbers and the animals themselves may often be observed. In the northern and central parts of the Betpak-Dala desert, with the formation of the snow cover, the corsac foxes begin to suffer from a great insufficiency of food, since of the rodents, only the red-tailed gerbil remains active and they rarely come out of their burrows at that time. Therefore, corsac foxes here in winter migrate after saiga herds, feeding on the carcasses of antelope killed by wolves or starvation. The animals move at night. Each year in December, saigas move to the southeast for 4 to 5 days through the central region of the Betpak-Dala; in this short period or a bit later, the corsac foxes also migrate. By the end of December, the majority of corsac foxes have already followed the trail of the saigas southward to the Chu river valley. Those remaining suffer greatly from hunger. There are no rodents, and, at this time, the remains of saiga carcasses killed by wolves, foxes and corsac foxes also disappear. The last animals remain without prey and are also forced to migrate, following the saigas. Moreover, in places of massive saiga concentrations, the snow is much beaten down and trampled by them, which facilitates the movement of corsac foxes and their capture of rodents. Many corsac foxes die from starvation and wolves. In winter in Trans-Baikaliya and the Mongolian Republic, corsac foxes follow the migrating herds of Mongolian gazelles (Brom, 1952 and others).

305 The cause of corsac fox migrations may also be steppe fires, which cover great areas. Migrations explain their appearance in the regions, where in summer they are absent or rarely met with. For instance, in a series of regions in Kokchetav district, they are found only in winter, appearing there at the end of December. The magnitude, and often also the distance of migration, depend upon the number of corsac foxes and the degree of change in conditions which induces migration (much snow, frozen crust, cold, steppe fires, etc.).

Corsac foxes migrate also in the east—in Pri-Baikal, Trans-Baikaliya and the Mongolian People's Republic. Thus, in some years, they appear in the Selenga river valley in Kyakhtinsk district, penetrating there from the MPR (Fetisov, 1949; Surmach, 1957). In southeastern Trans-Baikaliya, during the time of winter migration, corsac fox sometimes transgress very far to the north and appear in forest-steppe regions (Aleksandrozavodsk region—Algachi, Man'kovo, Bokhto and Bazanov; Stretensk region—Kuenga river, left tributary of the Shilka; E. Pavlov, 1949; N.V. Nekipelov). In the last decades, mass appearance of corsac foxes in Trans-Baikaliya was noticed in 1946–1947 and in 1955. The main reason for the mass appearance of corsac foxes in Trans-Baikaliya was their migration from the northeastern part of the Mongolian Republic, where in 1942/1945 and in 1953 there was in places mass reproduction of Brandt's vole, which later disappeared, that provoked the mass migration of corsac foxes northward (N.V. Nekipelov). In Trans-Baikaliya, corsac foxes migrate, moving out from regions where Brandt's vole and Daurian pika populations are reduced. In Trans-Baikaliya, the corsac fox migration is more rarely caused by deep snow cover (Cherkasov, 1884; Dorogostaiskii, 1935, Podarevskii, 1936).

Extinction of rodents or other unfavorable conditions cause mass migration and settlement of corsac fox even beyond the range boundary. In this way, they sometimes populate new territories, but, as a rule, not for long. Thus, in separate years corsac foxes appeared in the middle Volga region, where they were hunted in 1930 and 1933 in the Bol'sheglushitsk region. They also transgressed in 1936 into the Bol'shechernigovsk region (Dobrokhotoy, 1937).

In the severe heavy-snow winter of 1955/56, corsac foxes appeared in the forest-steppe of the Volga region at Vol'sk city and Teplovka village, arriving, apparently, from the Trans-Volga steppes.

Transgressions hither of corsac foxes there are so rare that none of the old-timers remembers such an immigration (Kirikov, 1959). In the winter of 1943/44, corsac foxes were encountered in Oktyabr'sk, Bugul'minsk and Bavlinsk regions of the Tatar ASSR, where they had not previously been observed (Popov and Lukin, 1949). In order to reach the regions mentioned, the animals must have traversed not less than 320 km in a straight line. In the 30's of this century corsac foxes were caught in the Beloretsk region in Bashkiria, 280 km from the border of their permanent range. In the past century, corsac foxes appeared beyond the Ural range, in the Shadrinsk region, 240 km north of places where they usually occur (Sabaneev, 1874). In the winter of 1948/49, when the snowfall was heavy in Kazakhstan, corsac foxes were caught in Sorochinsk, Perevolotsk, Krasnokholmsk, Orenburgsk, Burtinsk, Troitsk and other regions of Orenburg district, 200 km and more to the north of the core habitat (Darkshevich, 1950). In 1952, there were many corsac foxes in Chelyabinsk district, whence they arrived from Kustanai and Severo-Kazakhstan districts. The same was also observed in western Siberia, where the corsac fox penetrated northward to Lebyazh'ir in Kurgan district, Tyukalinsk, Tara and Vengerov which are 50–200 km beyond the usual northern limits of their distribution (Shukhov, 1928; Kirikov, 1959, 1960).

Massive emigration of corsac foxes from the steppes of Kazakhstan to the forest-steppe of western Siberia took place at the end of the 10's and start of the 20's and especially in the 40's of the current century. The First World War and the Civil War which followed it distracted many hunters from the fur harvest. The corsac fox catch was greatly reduced. At the same time, the fields were badly treated. It was not possible to harvest and thresh the ripened wheat; much arable land was abandoned, allowing mass reproduction of rodents in them. Under-harvest of corsac fox and the wealth of food reserves favored its reproduction and intensive colonization beyond the usual limits of the range. In 1917, corsac foxes appeared in great numbers in the Barabinsk steppe east of the Irtysh. Their number increased without pause until 1921. Thereafter, their population began to decrease, and by 1929 they completely disappeared (Sludskii, 1930).

In the Altai territory, in the territory of the Kiprinsk region, corsac foxes were common up to 1916, then disappeared. In the winter of 1920/21 in this region, a mass appearance of this animal

was noted, moving to the north. By the end of the 20's, corsac foxes disappeared there (Velizhanin, 1931). The same picture was also observed southward—in Semipalatinsk district (Selevin, 1930).

Migration of corsac foxes also takes place in deserts, where it is associated with prolonged, continuous snow cover accompanied by mass death of ungulates. After the heavy-snow winter of 1949/50, corsac foxes appeared in great numbers south of Zapadno-Kazakhstansk and Aktyubinsk districts and penetrated to the northern shore of the Caspian. Already in December 1948, many of these animals arrived from the north in the Syr-Dar'ya river valley (Sludskii, 1953). The corsac fox passed through from the north in significant numbers to Dzhambulsk and Alma-Atinsk districts and to the Chu valley. They appeared not only in the foothills but also low in the mountains. With the formation of deep snow cover, they began to return again to the sands of the Pri-Chuisk Muyunkum, but there was also much snow there, and the animals died of starvation.

At the time of emigration from the northern deserts, corsac foxes crossed the ice of [Lake] Balkhash and appeared in southern Pri-Balkhash (winters of 1938/39; 1943/44, 1945/46, 1948/49 and especially 1950/51). In the foothills of the Dzhungarsk Alatau and in the Alakul' depression, corsac foxes appeared in 1938/39, 1947/48 and 1948/49, i.e. in nearly the same winters as in southern Pri-Balkhash. In Zaisan depression, the corsac fox population sometimes increased on account of the animals emigrating hither from Xinjiang, which took place in November–December 1938. During the time of emigration of corsac foxes from northern-type deserts southward from the southern edge of the semideserts to the foothills of the Tien Shan, they traveled a straight-line distance of 400 to 600 km.

With food scarcity or difficulty in obtaining it, corsac foxes approach populated places, even large cities. Thus, in the severe winter of 1939/40, in Pavlodarsk district, they were encountered in great numbers near settlements, and regularly fed on meat-packing wastes near the city of Pavlodar. In the heavy-snow winter of 1940/41, in Severo-Khazakhstansk district (Sovetsk region, near Barankul' settlement), corsac foxes appeared in such great numbers that one hunter obtained more than 50 animals in the season. In the winter of 1948/49, in Karaganda district, corsac foxes and red foxes often appeared on the outskirts of settlements and within

the precincts of Karaganda, where they fed on rubbish; several emaciated animals were caught by hand.

Therefore, for the corsac fox in its whole range, it is characterized by considerable displacement, governed, first of all, by periodic food deficiency. In the forest-steppes, steppes, semideserts and deserts, the corsac fox performs migrations almost yearly. The direction of migration changes, but more often the animals go southward, rarely to the north or other directions. Distances traversed by corsac foxes during times of migration are not established, but the boundary of the range, in connection with emigration, "pulsates" within limits of 50–600 km. As a result of migration and emigration, the corsac fox population in one or another region may change as much as ten fold.

Reproduction. The corsac fox is monogamous, the male also participating in nurturing the young. Apparently, having formed a pair, corsac foxes live together until one of the members dies. In the Moscow zoo, a male living with two females in one cage covered [mated with] only one of them. In the course of a year only one litter occurs.

In Kazakhstan, in the steppe zone, rut in these carnivores starts in February; in the semidesert and desert zones—in January or the beginning of February; and in the steppes of southeastern Trans-Baikaliya, in February. At the time of rut, in the tracks orange-red spots are often met with, left in those places where the animal urinated. Two corsac foxes usually live near some burrows. The animals usually rut at night; at this time their peculiar barking is often heard. Several males run behind a female in heat for the first time, or for one left barren for some reason, and fight usually occurs between them. The female usually mates in the burrow.

The duration of pregnancy is not accurately established, probably equaling 52 days on the average. The earliest litter was found in Aktyubinsk district on 15 March 1953. In central Kazakhstan, at Lake Tengis, on 11 April 1957, a female was caught with 12 embryos, the body length of which equaled 10 cm and the average weight, 30 g. In Kustanai district, the first litter was found on 25 April, and between 5–15 May the young corsacs came out from the burrow. In Kokchetav, Tselinograd and Ural'sk districts, the young appeared at the burrows on 15–25 April. In Semipalatinsk and Vostochno-Kazakhstansk districts, they begin to emerge on 5–10 April. In southeastern Trans-Baikaliya, a recently parturient female

was caught on 16 April 1961 (N.V. Nekipelov). Litters here appear at the end of April—beginning of May (Peshkov, 1954). In the Moscow zoo, pupping of the corsac fox was observed eight times—between 18 March and 10 May. From Table 37, one may judge litter size, and when young began to emerge from the burrows. On 10 June 1942, in the Zharminsk region of Semipalatinsk district, 16 young of the same age were dug out from a burrow.

Therefore, in Kazakhstan, there may occur in a corsac fox litter from 2 to 16 young, but more often 3–6 (average of 5 for 100 samples). In the northeastern Cis-Caucasus, three young animals were found in a burrow (Heptner and Formozov, 1941). In the ephemeral deserts of Uzbekistan, the litter usually consists of from

Table 37. The number of young in one litter of corsac fox in Kazakhstan

Zones and districts	Number of pups in litter	2	3	4	5	6	7	8	9	10	Total litters	Average number in litter
		Number of occurrences										
True steppes:												
Kustanaisk, Severo- Kazakhstansk, Pavlodarsk [districts]		1	8	6	2	7	2	2	—	1	29	4.9
Dry steppes:												
Ural'sk		—	2	3	5	2	—	—	—	—	12	4.6
Aktyubinsk												
Kokchetav and Tselinograd		—	8	8	6	10	3	2	1	—	38	5.0
Semideserts:												
Karaganda		—	—	—	4	1	5	1	—	—	11	6.3
Vostochno- Kazakhstansk and Semipalatinsk		—	2	1	4	—	2	—	—	—	9	4.9
Deserts:												
Dzhambul		—	1	—	—	—	—	—	—	—	1	3.0
Total		1	21	18	21	20	12	5	1	1	100	5.0
in %.		1	21	18	21	20	12	5	1	1	100	

3-4 young, but many of them die while still in the burrow. The reason for juvenile mortality in the burrow period of life is believed by many hunters to be due to ants which attack the still-helpless animals. They also point to the possibility of diseases (Suleimanov, 1939). In the steppes of southeastern Trans-Baikaliya, the litter contains from 5-7, and up to 10, animals (Cherkasov, 1884; Peshkov, 1954). In the Mongolian Republic, in the Kerulen valley on 22 May 1944, 7 young were found in an excavated corsac fox burrow (Skalon, 1949), and in Choibalsan region, on 24 May—11 pups half the size of adults (Kucheruk and Dunaeva, 1948). In the Mongolian Republic, the number of young animals in the litter varied from 2 to 12 (Bannikov, 1954). In the Moscow zoo, in five litters there were 3, 4, 5, 6 and 7 young.

It is not known whether fertility of corsac foxes increases significantly in years of food abundance as happens, for example, in arctic foxes, although the larger litters were found in the years with abundant sagebrush voles or Brandt's voles.

Growth, development, and molt. Corsac pups are born blind and with closed ear passages. They are covered with a light brown fluffy pelage. The tail is monocolored, while in the red fox its tip is always white. The tone of their fur becomes increasingly more and more yellow with age.

Weight of newborns is 60-65 g; body length, 13.5-14.0 cm. They can see on day 14-16. At 28 days of age, they begin to eat meat (E.A. Petrova). They grow rapidly. Thus, in central Kazakhstan young animals—females caught on 28 May 1960, weighed 245-262 g and of corsac pups from a litter captured on 29 May 1960, males were 392-400 g and females, 378-405 g. In this same region, two young females caught on 31 July 1951 each weighed 1900 g already, and a male caught on 3 August 1951—2050 g. In the Betpak-Dala desert, a young female caught on 11 May 1955 weighed 1250 g, and a male caught on 17 May 1956—1200 g. Young females also captured there weighed: 20 September 1957—1800 g, and 13 December 1957—2000 g. In Turkmeniya, on the southern edge of the Karakum, a young animal caught on 6 May was half the size of an adult. Weight of such an adult female is 2.3-2.5 kg, and of male, up to 2.6 kg. Consequently, at the beginning of May in Turkmeniya and the middle of this month in the northern deserts, young animals already have attained half the dimensions of adults. Farther north, they are smaller in May. However, already by the

beginning of August, the young weigh 1900–2000 g, i.e. slightly less than adults, even in the semidesert. Apparently, the corsac pup completes its growth in 4–5 months.

In the den burrow, the female lives excellently with the pups until they are 2 months of age. The male, though he participates in the raising of the young, apparently rests in another burrow or outside it, since in no case has he ever been found in any shelter with the pups (sample size is still small). When the pups approach full growth, the female sometimes lives with the male in one burrow, while the young are in a neighboring one.

In spring and summer, many fleas are found in occupied corsac fox burrows (Brom et al., 1948), which greatly bother the animals. Apparently, because of the parasites and dirt in the burrow, the female changes burrows 2–3 times, carrying the young with her.

The young disperse early. Out of nine burrows with young, excavated in June–August, in only one burrow were two young revealed, while in the remainder, only one. Young and adult corsac foxes also change burrows often.

In burrows excavated in November–December, 2–5 young animals were often found (Dinnik, 1914; Sludskii, 1930, 1939; Heptner, 1932). On Barsa-Kel'mes island, in December, three young males were caught in one burrow, and in a second—three males and one female (Sludskii, 1939). Apparently, with the onset of cold, the earlier dispersed young corsac foxes gather again in one burrow. It is not known whether they live in groups during the course of the whole winter, though there are references to litters of corsac foxes that separate only at the time of onset of rut (usually in February) or in spring. Assertions that several adult animals may live peacefully in one burrow require verification.

309 Duration of lactation is not established; a female caught in Betpak-Dala on 17 May in a burrow with three young that weighed 1200 g already had no milk in her glands and her teats were dry.

Females attain sexual maturity at the age of 9–10 months. In 28 animals investigated at the age of 4 months, there were 53.4% males and 46.6% females. Under favorable conditions, the corsac fox becomes more fertile and therefore its numbers may quickly increase.

It is accepted that the corsac fox molts two times per year—in spring and autumn. In spring, the winter pelage is completely replaced; it is not established whether the pelage is also completely

replaced in autumn or not. By the end of winter, the hairs lose their luster; gradually dulling, the guard hairs become dry and frayed and their ends bend. First of all, fur on the head and limbs is replaced, then fur on the nape and shoulders molts, later the anterior part of the back, side and thigh, then the posterior part of the back and, last, the rump and tail. Consequently, in spring the molt proceeds from head to tail. Spring molt lasts quite a long time. In the northern deserts (Barsa-Kel'mes Island), it is already initiated by February 15 and lasts until the middle of May. In a nursing female caught on 17 May 1956 in Betpak-Dala, the winter fur was nearly fully shed, and was retained only on the sides, rump and tail. Animals caught in this desert in August had summer fur, while those captured in the beginning of November well exhibited new fur, but it was still not mature. The growth of the [winter] pelage ends only at the end of November, just after severe cold makes its appearance.

Consequently, growth of winter fur is in reverse order. First growth commences on the tail and rump, then on the thighs and back, further on the nape and sides, and lastly on the paws, belly and head.

Enemies, diseases, parasites, mortality and competitors. Everywhere within the boundaries of the Soviet Union and the Mongolian Republic the competitors of corsac fox as regards food are the wolf, red fox, and steppe polecat [*Mustela eversmanni*] and in the forest-steppe and steppe zones, also ermine and weasel; in the Barabinsk steppe and in Trans-Baikaliya—kolonok [*M. sibirica*] and in the latter region the solongoi [*M. altaica*] as well. In central Kazakhstan and in Trans-Baikaliya among the competitors of the corsac fox is also considered the manul [*Felis manul*] and in the deserts—marbled polecat [*Vormela peregusna*], steppe [*F. s. libyca*] and sand [*F. margarita*] cats, jackal and several others.

In the spring-summer period, wolf feeds mainly on the same rodent species on which the corsac fox feeds, and is very common in some places. By comparing fur tanning of both species, one may see that in the Tselinograd district, for each corsac fox caught, there was 0.5 wolf and in Karganda district, 1.4 wolves. Red fox is an especially dangerous competitor for corsac fox. Throughout the whole year, it feeds on the same food as corsac fox. It is stronger than the corsac fox and more successfully catches rodents of moderate and large size; it is also better adapted to mousing in regions where the snow cover reaches 10 cm and more. Only in

the semideserts does the corsac fox, apparently, hunts more successfully than the red fox. The red fox is ecologically more plastic than the corsac. In northern Kazakhstan, judging by fur tanning data during recent years, the red fox is numerically predominant over the corsac fox. Thus, in Kustanai district, 2000–3000 red foxes are caught and only 500–800 corsac foxes, in Severo-Kazakhstansk, 2000–2400 red foxes and only 100–300 corsac foxes, and in Pavlodarsk, up to 2500 red foxes and 1000–1500 corsac foxes.

In semideserts, before ploughing of virgin soil, corsac fox obviously predominated over red fox. In Tselinograd district, for example, in the 30's of the current century, only some tens of red foxes and more than a thousand corsac foxes were caught. In the 40's, already 400–500 red foxes were caught and 1000–1200 corsaa. In the 50's, the population of red foxes greatly increased and together with this the maximum catch; in a season, 2900 fox skins were prepared and at the same time 2400 corsac fox skins. Therefore, competition between these two species of carnivores rapidly
 310 increased. In northeastern Cis-Caucasus, in the season of 1924/25, one hunter took 15–30 corsac foxes and 10–20 red foxes (Heptner and Formozov, 1941).

In the northern deserts, the red fox population was always much higher than the number of corsac foxes. According to tanning data, in Kzyl-Ordinsk district, 4 to 5 thousand red foxes are caught, maximum 8 thousand, and corsac foxes—200–400, up to 900 individuals. In Alma-Atinsk district, the corsac foxes are still fewer: during the last ten years here, the maximum catch of red foxes reached 15 thousand, and corsac only 650 individuals. In the steppes of Trans-Baikaliya, corsac fox populations are predominant over red fox.

Therefore, in virgin dry steppes and semideserts, corsac foxes predominate, and in deserts—red foxes. Ploughing of virgin lands leads to disappearance of corsac fox and growth in numbers of red fox, of which the Ukrainian steppes, and in recent years—also Kazakhstan, are obvious examples. Competition between red and corsac foxes for food becomes particularly intense in autumn and winter, when the majority of rodents enter hibernation, many birds migrate, and reptiles and insects are torpid.

Throughout the range of the corsac fox, the steppe polecat is numerous, also a serious competitor of the corsac fox. In the 30's of the present century in Kazakhstan, up to 500 thousand skins of

this carnivore were taken every year; i.e. one hundred times more than corsac foxes. The intensity of competitive relationship between these animals can be partially judged by the frequency of their capture in traps at tarbagan marmot burrows. For a series of years in eastern Trans-Baikaliya, during the warm months, 105 corsac foxes, 4 wolves, 9 weasels, 67 solongoi, 412 steppe polecats and 8 badgers were caught in traps set for marmots (Brom et al., 1948). For every corsac fox, four polecats were obtained. Ermine, weasel, kolonok, solongoi, marbled polecat and wild cats, because of their relatively low number and small size, are not considered as serious competitors of the corsac fox. The corsac fox itself rarely attacks small carnivores.

Among avian competitors of the corsac fox are manifested saker falcon (*Falco cherrug*), pallid and northern harrier (*Circus macrourus* and *C. cyaneus*), steppe eagle (*Aquila rapax*) and rough-legged buzzard (*Buteo lagopus*). In the western range, the long-legged buzzard (*Buteo rufinus*) appears as a competitor of the corsac while in the east—in Trans-Baikaliya and the Mongolian Republic, it is the upland buzzard (*Buteo hemilasius*). The steppe eagle and, rarely, the upland buzzard are enemies of the corsac fox and with regard to saker falcon and common buzzard [*Buteo buteo*], this animal becomes a commensal (see above).

The wolf is the greatest danger to the corsac fox. In the second half of winter, especially with much snow, wolves kill many corsac foxes (Velizhanin, 1931). Thus, in Tselinograd district, in the winter of 1947/48, in February, one hunter found six corsac foxes torn apart by wolves. In Semipalatinsk district, in March–April 1948/49, a hunter found the remains of 10 corsac foxes eaten by wolves, and in the winter 1950/51, in the Kurchumsk region, in one day, remains of five corsac foxes eaten by wolves were found. Wolves attack mainly animals weakened by starvation, or eat their dead bodies. They rarely catch healthy animals if these are near a burrow in which they can hide. A pursued corsac fox runs with a speed of 40–45 and up to 50 km/hour, but it can run thus for only 15–20 minutes. The desert wolf runs with a speed of 40–45 and up to 55 km/hour, but is more enduring and in open places, can catch the pursued corsac fox, especially if a group of wolves is hunting. In warm times [of year], wolves attack corsac foxes rarely, but even more rarely catch them. Thus in Betpak-Dala, the remains of corsac foxes were found in 0.8% of the wolf feces collected in

May–June (864 samples). In 101 stomachs of wolves caught in November–December in the same desert, corsac fox remains were found in only one. Wolves also destroy corsac fox litters, tearing apart their burrows (P.T. Kryzhinovskii). However, the attempt to excavate the burrow does not always meet with success.

311 The red fox also belongs among the enemies of the corsac fox. It destroys the corsac fox in winter when it suffers from food shortages. Cases of corsac foxes hunted by red foxes and carcasses of corsac consumed by red foxes are known in Kustanai, Severo-Kazakhstan, Pavlodar, Kokchetav and Tselinograd districts, i.e. in steppes and semideserts. Red fox attacks on corsac foxes were observed particularly often in the heavy-snow winters of 1947/48, 1948/49, 1950/51 and 1953/54. As a rule, hunters found corsac foxes killed by red foxes in March. With absence of food, red foxes attack corsac foxes earlier—in November and December (D.N. Boiko). In summer, red foxes destroyed den burrows of corsac foxes and killed the young. This was observed in the Oktyabr'sk region of Severo-Kazakhstan district and the Kellerovsk region of Kokchetav district (S.G. Chmut and D.P. Fomenko). Decrease in corsac fox numbers in the semideserts and steppes of Kazakhstan was related to the rapid growth of the red fox population, crowding out and destroying the corsac foxes, in the same way as the wolf. With abundant food, red fox and corsac foxes coexist with one another. They were observed together at carcasses of fallen livestock and shot saigas (Sludskii, 1930).

The corsac fox suffers also from shepherds and stray dogs. During the driving of livestock to and from summer pastures, thousands of hungry dogs, which harass and kill all animals and birds which they encounter on their way, go with the herds and flocks (Sludskii, 1961). Particularly dangerous are the Asiatic *borzois*—the *taza* and *vyborzka*—which catch up comparatively easily with corsac foxes. Dogs also destroy the burrows of this animal and wipe out the corsac pups.

The golden eagle (*Aquila chrysaëtos*) often attacks red foxes and with training successfully hunts corsac foxes. However, its influence on corsac fox populations is negligible. The steppe eagle [*Aquila rapax*] is a more serious enemy. Remains of corsac fox were met with several times near the nests of eagle and in their castings (Nasimovich, 1951). In some places, the steppe eagle is abundant and may kill a considerable number of corsac foxes.

Thus, in Kalmykia, in places where saigas give birth to young, 24 to 40 eagles were observed in one field of view (Dal' et al., 1958). In rare cases, the upland buzzard (*Buteo hemilasius*) attacks corsac
 312 pups (Nasimovich, 1951). In Semipalatinsk district, at the end of winter, remains of three corsac foxes were found eaten by an eagle owl (*Bubo bubo*). In winter, in the forest-steppes, steppes and semideserts, the snowy owl (*Nyctea scandiaca*) may attack the corsac fox.

Diseases of corsac fox remain nearly unstudied. It is known only that they suffer from rabies and carnivore distemper. In 1950 and 1951, a distemper epizootic spread over the whole territory of Gur'ev and Zapadno-Kazakhstan districts, the western half of Aktyubinsk district, and adjacent Astrakhan, Volgograd, Saratov and Orenburg districts. In this vast territory, mass mortality was simultaneously observed in corsac fox, red fox, wolf, raccoon dog, steppe polecat and even dogs. Mortality of corsac foxes from carnivore distemper was noted in 1950 in the Chapaevsk region of this same area (Sludskii, 1954). Summer mortality of corsac foxes from an unknown infection occurred in places in the Kurchumsk region of Vostochno-Kazakhstan district at the end of April 1948, and in July–September 1951 also in the Leninsk region of Severo-Kazakhstan district, where separate hunters found up to three fallen animals. Rodent plague, induced by *B. pestis** has not yet been established in corsac foxes, though several hundred corsac foxes were examined in the regions where plague is endemic.

In a young corsac fox, caught in the Sovetsk region of Severo-Kazakhstan district on 27 July 1941, the neck and head were heavily infected with ticks (species not determined). The following four species of fleas were noted on animals from central Kazakhstan: *Pulex irritans* (large numbers), *Ctenocephalides canis* (rarely encountered), *Ceratophyllus tristinus* (rarely encountered) and *Ctenophthalmus breviatus* (rarely encountered). The first two flea species are specific parasites of carnivores and of the latter two, one is a parasite of ground squirrels and the other, of voles (Mikulin, 1956).

In southeastern Trans-Baikaliya, for a series of summers in May–October 6, 413 fleas were collected from 105 corsac foxes between May and October, from which were identified (in % of total): *P.*

*Now *Yersinia pestis*—Sci. Ed.

irritans L.—70.2; *Oropsylla silantiewi* W.—3.7; *Chaetopsylla homoeus* Rh.—5.3; *Frontopsylla elata luculenta* J. et R.—2.0; *Ctenophyllus hirticrus* J. et R.—11.7; *Rhadinopsylla dahurica* J. et R.—3.0; *Amphalius runatus* J. et R.—3.2; *Ceratophyllus tesquorum sungaris* J.—0.1; *Neopsylla bidentatiformes* W.—0.2; *Neopsylla pleskei orientalis* J. et Arg.—0.05; *Ophthalmopsylla praefecta* J. et R.—0.2; *Frontopsylla wagneri* J.—0.07; *Pectinotenus pavlovskii* J.—0.07; *Paraceras flabellum* W.—0.01; *Archaeopsylla sinensis* J. et R.—0.07; *Ceratophyllus calcarifer* W.—0.03; *Amphipsylla vinogradovi* J.—0.01.

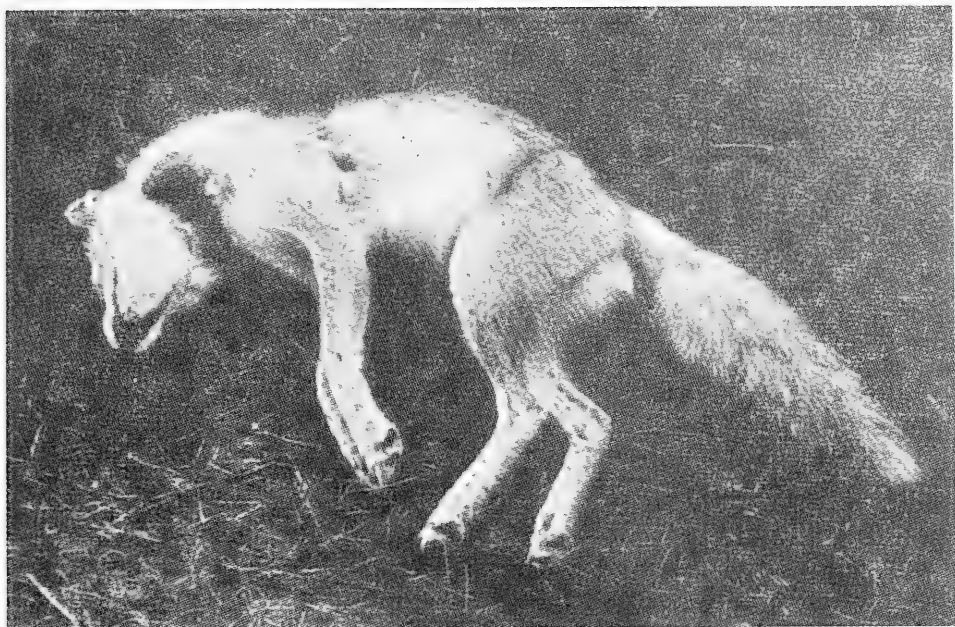
Fleas not specific for carnivores and which parasitize mainly rodents in Trans-Baikaliya, occur on the corsac fox and are assignable to 13 species and constituted 24.5% [of the total] (Brom et al., 1948). In southeastern Trans-Baikaliya, the average number of fleas parasitizing a corsac fox were: in April 3.0, in May 35.3, in June 10.9, in July 37.0, in August 32.4, in September 84.8 and in October 188.9 individuals. In corsac fox burrows, there are many fleas. Since a great number of fleas parasitize the corsac fox, it is probable that it acts as a vector of fleas infected with plague (Brom et al., 1948).

The mortality rate among corsac foxes from various factors is not known. Especially many of them die, apparently, from food shortage caused by the decreases in rodent populations or their unavailability due to the deep snow cover, or hard-crusted snow, or ice.

In Kazakhstan, many corsac foxes died from starvation in the winters with prolonged snow cover of 1940/41, 1947/48, 1949/50, 1950/51 and 1953/54. Thus, in January 1949, in the Dzhurinsk region of Aktyubinsk district, one hunter found 5 corsac and six red foxes dead from starvation. Starving animals allowed humans to approach them and they could be caught by hand. In southeastern Trans-Baikaliya, the deep snow cover is also fatal to corsac fox.

313 Food shortage in winter in some years is manifested as the most important factor in corsac fox mortality, leading to a population decrease.

Population dynamics. In one or another region, often very broad, the numbers of corsac foxes is subjected to great annual changes. In years with abundant food, their populations rapidly grow so long as unfavorable conditions of existence do not occur. Population growth may be very rapid. In 1930, on Barsa-Kel'mes



311 Fig. 114. Adult corsac fox with throat crushed by red fox near its burrow. Badkhyz Preserve, southern Turkmeniya. 28 April 1962. Photograph by A.A. Sludskii.

Island (Aral Sea), where the corsac fox was absent, 3 males and 2 females escaped from cages. In 1933 and 1934, 77 corsac foxes—the whole population—were caught, which had increased 15 times in 3–4 years (Sludskii, 1939).

Among the factors reducing the corsac population is a small number of rodents—voles and pikas in the northern half of the range and gerbils in the southern desert parts—as well as their unavailability due to the deep snow cover (deeper than 15 cm) or the formation of hard snow crust or ice. At this time, corsac foxes go hungry, become weakened and die in great numbers from starvation, enemies (wolves, red foxes) and diseases. Reduction of the population usually is carried out in one season.

In the northern Caucasus at the end of the nineteenth century, the corsac fox was considered a very rare and vanishing species (Dinnik, 1914; Satunin, 1945). However, in 1921–1925, many of the animals were found there: One hunter caught 15–30 corsac foxes each season during that time (Heptner and Formozov, 1941). During 1926 and especially 1927, the corsac fox population decreased

greatly and from 1932 to 1944 their skins were not prepared for tanning. From the 40's the corsac population there gradually grew, and then rapidly increased to 1951. However, in 1952, their number again fell catastrophically (Vereshchagin, 1959). The cause of the drop in the corsac fox population in the Cis-Caucasus was strong *dzhut* [extensive periods of continuous snow cover] (1949/50, 1950/51, 1952/53).

In the steppes and semideserts of Kazakhstan, judging by the delivery of corsac fox skins to the Irbit'sk fair, at the end of the 19th century, its number fluctuated 15-fold. In the period from 1880 to 1895, it was lowest in 1880, 1890 (in 1881,* only 5 thousand skins were delivered to the fair and in 1890, 2 thousand; both times were after the heavy *dzhut* of 1879/80 and 1888/89). The highest populations occurred in places in 1883—1886; in 1884, 30 thousand skins were delivered to the fair, and in the following years, 25 and 15 thousand skins.

In the forest-steppes of western Siberia (Orenburg, Chelyabinsk, Om'sk and Novosibirsk districts) and in the northern steppe zone of Kazakhstan (Kustanai, Severo-Kazakhstan, Pavlodar, Semipalatinsk and other districts), the corsac fox had nearly disappeared by 1910 (Korsakov, 1938), and reappeared again in 1916—1917. Its numbers reached a peak in 1923.

In the dry steppes and semideserts (Ural'sk, Aktyubinsk, Tselinograd (the former Akmolinsk), Karaganda and other districts), the corsac fox began to appear in considerable numbers from 1919 on. Before this year, the inhabitants of Tselinograd district did not know of it. It became especially numerous in 1921 and 1922, but in 1923, the population began to fall rapidly and by 1924, this animal had again become rare.

Intensive reproduction of the corsac fox in the beginning of the 20's was attributed to several factors. In connection with the First World War, followed by the Civil War, the number of hunters sharply decreased and the hunting economy nearly stopped around 1920—1921, i.e. for 7—8 years. Many fields were abandoned and in them there was strong reproduction of rodents. In these same years in the steppes many livestock, especially horses died. All of this favored the rapid growth of the corsac fox population, and it quickly spread in all Kazakhstan and adjacent areas. In these years,

*From context, probably should read 1880—Sci. Ed.

in Kustanaisk, Severo-Kazakhstan and Pavlodar districts, individual hunters took 150 to 200 corsac fox skins per season. After the peak population (1921–1923), 225,445 skins were exported from the USSR in 1923–1924 and 1924–1925—a record number for the entire period of existence of the trade (Kaplin, 1960).

The rapid decline in the corsac fox population in the middle of the 20's was the result of hunting of carnivores and the ploughing of fallow and virgin lands. After the end of the Civil War, many hunters returned to peaceful occupations and the steppes were flooded with agents of tens of tanning organizations which rapidly drove up the price of furs. At this time "everyone who was able went to the steppe with tools, weapons, shovels and barrels filled with water and ruthlessly proceeded to kill the little foxes in great numbers, digging and smoking them out of burrows in groups. This barbaric 'hunting' was practiced especially intensively at the beginning of winter with the first snowfall, when it was easy to find the corsac burrows through their tracks" (Selevin, 1925). This rapacious taking of corsac fox was also carried out in western Siberia where, moreover, the animals were pursued on horses with or without dogs, and poisoned with strychnine. As a result, at the end of the 20's, the corsac fox in many places in Kazakhstan and western Siberia was "almost completely exterminated" (Zverev, 1932). Thus, in Semipalatinsk governance in 1921/22, 1785 corsac skins were tanned; in 1922/23—8,012; in 1923/24—19,344; in 1924/25—2,312; in 1925/26—503; in 1926/27—345; and in 1927/28—only 165 (Selevin, 1925, 1930; V.E., 1928). Overall, in four years, the corsac population had decreased 117 times. In Kazakhstan (as a whole) in 1924/25, 23,194 skins were tanned; in 1925/26—19,426; in 1926/27—7,934; in 1927/28—4,024; and in 1928/29—505 (Grossman and Kogan, 1932). In the following years, its harvest was prohibited.

Mass reproduction of the corsac fox, which was observed in the 20's of the present century occurred more or less simultaneously over a vast territory. A similar picture of reproduction in the 20's and subsequent decrease in their population was observed in the Cis-Caucasus, lower Volga region, forest-steppes of western Siberia, and Kazakhstan. An analogous picture was observed in some places in Turkmeniya. Thus, at the beginning of the 20's on the plains at the foot of the Kopet-Dag, corsac fox almost completely disappeared as a result of the application of strychnine. At

one poisoned carcass, as many as 13–14 corsac foxes were picked up in a night (V.G. Heptner).

In the steppes and semideserts of Kazakhstan, the corsac fox again began to appear in the middle of the 30's. Thus, in Kustanai district in the northern regions, it appeared in 1935, but was still absent in the Semiozernii and other regions, where it appeared in small numbers (Naurzumsk preserve) in 1936. Only in the heavy-snow winter of 1940/41 did corsac foxes here become numerous, migrating from neighboring regions. A new population peak (judging by tanned skins) in northern Kazakhstan was in 1938/39. In Kzyl-Orda and Chimkent districts, the corsac fox was especially numerous in 1934 and 1935.

The rise in the corsac fox population in the 30's in Kazakhstan stopped in the winter 1939/40 when, in many areas, the animals suffered from a sharp food insufficiency. After this winter, the corsac population in the north of Kazakhstan, judging by tanned skins, decreased nearly two times. It continued decreasing throughout the whole of Kazakhstan after the severe heavy-snow winter of 1940/41. But in 1944, nearly everywhere in Kazakhstan, the number of corsac foxes again increased and they were particularly numerous in the dry steppes and semideserts of Kokchetav, Tselinograd and Karaganda districts. At the beginning of the 40's, the corsac fox population also began to increase in the forest-steppes of western Siberia, and it appeared in regions where they had long been absent (Makushinsk region of Kurgansk district, Sargatsk region of Omsk district and others).

In February–March 1948, in the northern and central parts of Kazakhstan, corsac foxes died in great numbers from starvation (voles were few). The winter of 1948/49 had exceptionally deep
 315 snow, and again many animals died from hunger and enemies; the corsac population greatly decreased (Sludskii, 1953). In this winter, corsac foxes appeared in significant numbers in the steppes and forest-steppes of Orenburg district (Darkshevich, 1950). In the 50's of this century in the northern steppes of Kazakhstan, an increase in the corsac fox population was observed in 1952, but they were especially numerous in 1956. In 1955/56, corsac foxes were also numerous in the steppes of Altai territory. After the severe winters of 1948/49 and especially 1950/51, corsac foxes appeared in relatively high numbers in the northern foothills of the Tien Shan in Kirgiziya and in southeastern Kazakhstan.

Subsequent significant decrease in corsac populations in the northern, central and southern regions (Betpak-Dala desert), induced by the absence of the sagebrush voles and other rodents, took place in the winter of 1959/60. In the 1960/61 season, there were few corsac foxes anywhere. In Kazakhstan as a whole, tanned corsac skins fluctuate approximately 15-fold.

In the deserts of the southern type (ephemeral), judging by the data on tanned furs, the highest population of corsac fox between 1950 and 1959 was in Uzbekistan in 1950 and 1956–1959, and in Turkmeniya during the time from 1948 to 1959—in 1952 and 1956; and the lowest—in Uzbekistan in 1955 after the severe *dzhut* of 1953–1954, and in Turkmeniya, in 1948 and 1953. In the southern deserts, the amplitude of population fluctuations of corsac fox is less than in the steppes and semideserts. In Uzbekistan, tanned skins of this animal varied only 1.5 annually, and in Turkmeniya, 3.3 times.

In the Daurian steppes of southeastern Trans-Baikaliya, the corsac fox population varied 18-fold over nine years (from 1940 to 1948) (Yurgenson, 1955). Judging from tanning, the highest population of corsac foxes here was in 1946/47 and in 1955. The main reason for this population growth was migration from the Mongolian Republic. In separate areas of the steppes, the Trans-Baikaliya population of corsac foxes changed under the influence of local factors (N.V. Nekipelov): epizootics among tarbagan marmots, their extermination by the antiplague organization, mass reproduction of Brandt's voles and Daurian pikas favoring the growth of the food base of the corsac fox, causing increase in its population.

On the whole, the number of corsac foxes in the territory of the USSR changes annually by 10 up to even 100 times. The most considerable change in corsac fox populations is found in the forest-steppes and steppes, where with unfavorable conditions, they completely disappear over vast areas for several years. Populations are more stable in the southern (ephemeral) deserts. Before a population peaks, it increases for several years. The high population is maintained for 1–2 years, and then decreases sharply. True periodicity is not observed in variations of corsac fox populations. During the last 20 years, increases have followed after 2–4 years, usually after three years. The amount of tanned skins also fluctuates strongly.

316 *Field characteristics.* This animal is very similar to the red fox, but is two times smaller in size. In contrast to red fox, the fur

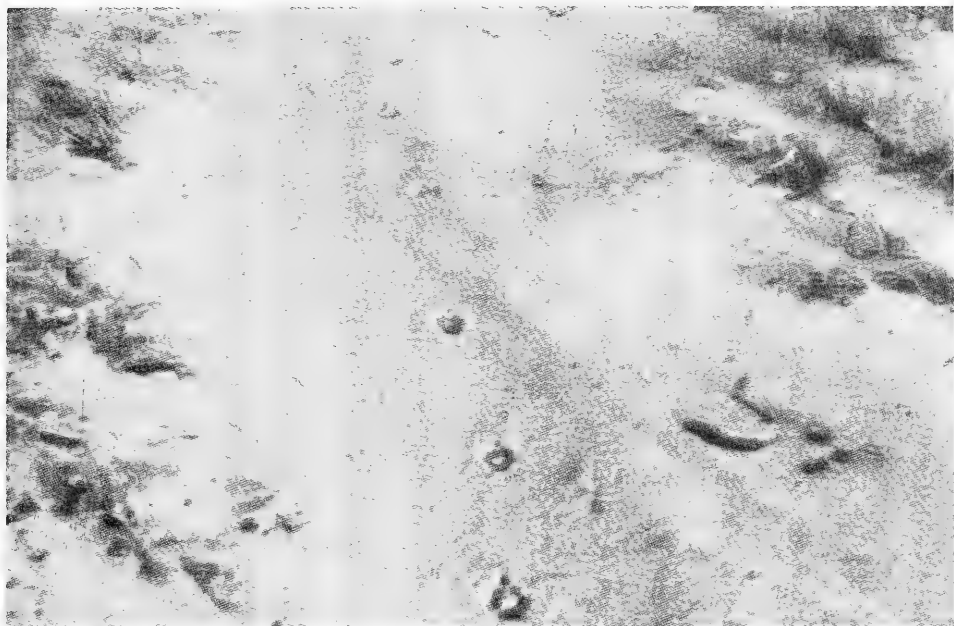


Fig. 115. Tracks of corsac fox. Left—track of Kazakhstan corsac fox, *V. c. corsac* L. (quite large form), on the snow in the vicinity of Dzhanibek (left bank of Volga), 20 October 1951. Right—track of Turkmenian corsac fox, *V. c. turkmenicus* Ogn. (small form), on wet sand. Karakum desert 100 km north of Ashkhabad, 21 January 1948. Sketch by A.N. Formozov, about 2/3 of the natural size.

color is uniform reddish gray. The tail is fluffy and long as in red fox and of one color, but does not have the white tip characteristic of the red fox. Ears are reddish-brown externally and not black as in red fox.

Tracks proceed directly—in a line. It steps precisely, track in track. The distance between tracks is 6 to 8 cm. The size of the footprint in the dust is 4×3 cm. At the entrance to the burrow, it levels the ground. Near the burrow there are always many feces—small sausages made up of mouse-like rodent hairs. As a rule, it is met with singly.

In the case of the appearance of danger, for example, when it notices a human near its burrow, the corsac “barks”. The agitated call of this animal is similar to the bark of a red fox, but at the same time is somewhat reminiscent of the mewing of cat and sounds like “m-yaaa”. A disturbed corsac fox also gives another call: “un! un! un!”. The cry “m-yaaa!” can be also heard at night in winter,



316 Fig. 116. Track of corsac fox on snow. Betpak-Dala desert. Kazakhstan.
15 December 1956. Photograph A.A. Sludskii.

when the animals feed on carrion, and also during the time of rut. Young animals at the age of 1.5 to 2 months, sensing danger, give a cry “vyau! vyau!” (A.S.)

Practical Significance

Corsac fox is a fur-bearing animal, but its fur is of low value, because it has quite coarse guard hairs. Previously its fur was more important. Harvest of this animal has been practiced for a very long time—in Kazakhstan, for example, since the Bronze Age (“Andronov culture”) and probably earlier. Later, corsac fox skins were used for a long time for payment of tribute. Thus, the nomads who inhabited Kazakhstan under Mongol subjugation in the 13th century were obliged to pay a tribute of furs, which included corsac fox skins. At the beginning of the 18th century the Tobol’ and Barabin Tatars delivered corsac fox skins as tribute (Kirikov, 1959, 1960).

From the ends of the 17th and 18th centuries, corsac fox skins were a subject of brisk trade between Kazakhs and Russians.

317 “Kirghiz-Kaisaks caught corsac foxes in the Zayaitsk steppe with golden eagle and dogs, and overtaking them on horses, killed with whips a multitude and they exchanged the whole lot, from 40 to 50 thousand, with Russians at Troitsk fort and in Orenburg. According to the Orenburg tariff, they were placed in value at 40 kopeks each.¹⁵ The Kirghiz, in their trade and exchange between each other, used them almost like money and the price of their goods was estimated according to the price of corsac foxes” (Rychkov, 1762; analogous information concerning the trade in corsac fox skins in Orenburg is contained in Pallas, 1773). At Yamyshev fort on the Irtysh and in Semipalatinsk, corsac fox skins were brought from Dzhungaria (which then included southeastern Kazakhstan) (Struve and Potanin, 1867). On the importance of corsac fox skins as barter, P.S. Pallas (1773) wrote that “As they (Kirghiz-Kaisaks; A.S.) had no money themselves, they evaluated everything with reference to horses and sheep, and instead of small coins, used wolf and corsac fox skins”. Harvest of corsac foxes was also developed in the 18th century in the forest-steppes of western Siberia (Pallas, 1786). In Kazakhstan, corsac fox skins were of great economic importance in the 19th century also. From 1857 to 1861*, from 5,213 to 14,546 corsac fox skins were exported annually from the Kirghiz steppe through the Petropavlovsk, Presnogor’kovsk, Omsk and Koryakovsk railway districts alone (Krasovskii, 1868).

In the 18th and 19th centuries, corsac fox trade was also developed in Trans-Baikaliya, where in the middle of the past century corsac fox skins were bought “from the first hand” for 50–60 silver kopeks per skin (Cherkasov, 1884) and exported to China, where they were in great demand. In the 60’s of the 19th century, a total 40–50 thousand skins were bought each year in Russia (Kaplin, 1960).

The size of the corsac fox catch in Kazakhstan and Middle Asia at the end of the 19th century can partly be judged by the delivery of skins to the Irbitsk fair (they were not sent to others). Sent (in thousands of skins) in 1881—5; 1884—30; 1885—25; 1886—15; 1887—5; 1888—15; 1889—4.5; 1890—6; 1891—2; 1892—6; 1893—6; 1894—8; 1895—5. By the end of the 19th century, the corsac fox trade was mainly harvested in the Aralo-Caspian lowland in the

¹⁵At that time the price of a sheep was 30 to 40 kopeks.

*In Russian original, 1961, a *lapsus*—Sci. Ed.

amount of “more than ten” thousand (Silant’ev, 1898; Turkin and Satunin, 1900).

In 1923/24, in the USSR, 135.7 thousand skins of this animal were tanned; in 1925/26—42.9; in 1927/28—12.2; in 1928/29—9,113 thousand. Thereafter, in the majority of regions, harvest was prohibited for a series of years. In 1940, 12 thousand were again tanned; in 1946—20.4; in 1951—21.8; in 1955—23.8 and in 1956—28.3 (Kogan, 1931; Kaplin, 1960).

In the beginning of the 20th century, about 15 thousand skins of corsac fox were imported annually from Mongolia to Kalgan [China] (Bogolepov and Sobolev, 1911), and in 1927—10,200; 1928—18,200; 1929—16,600; 1930—3,800 and 1931—24,000 (Blokhin, 1935). In this country, not less than 15–20% of the skins obtained remain in the hands of hunters (Bannikov, 1954).

In the late 20’s and early 30’s of the current century, the world yield of corsac fox skins ranged from 26 to 50 thousand, of which fewer than half were taken in the USSR, and more than 50% in the Mongolian Republic. Before 1938, the majority of corsac fox skins were exported from the USSR to England, USA, France and Germany. For 1923/24 and 1924/25, 225,445 skins were exported abroad for the sum of 1,783,107 rubles (Kaplin, 1960). The demand for corsac skins abroad increased greatly when in 1922/23, a method was discovered to dye them in various colors while preserving the silvery tips of the guard hairs.

In the 30’s, as a result of the severe drop in populations of this animal, tanning of its skins greatly decreased, and together with this exports declined. After the end of the Second World War, the reduction in demand for long-haired furs influenced the price of corsac skins—they were greatly reduced, as a result of which their
 318 export in 1951–1958 was no longer profitable. On the eve of First World War, a corsac fox skin brought 1.2 dollars on the external market, in 1923/25—3.85 and in 1943—5.80 for a skin of first sort of the Petropavlovsk type. In the following years, the price declined, and then began to rise again (Kaplin, 1960).

Earlier, in Kazakhstan and western Siberia, corsac foxes were caught in jaw traps, coursed with *borzoi* dogs and golden eagles, chased down on horseback and killed with whips and *soila* (long sticks), dug and smoked out of the burrows with smoke from burning sulfur or grass, or drowned with water. Lastly, they were poisoned with strychnine, nuxvomica, and other local poisons. In Trans-

Baikaliya, they were caught with jaw traps, "*bashmak*", *cherkan** and other traps which were set at the entrance to the burrow. At the present time, the main mass of the animals is caught with No. 3 and No. 5 jaw traps and they are rarely coursed with dogs.

The corsac fox is not a significant threat to small-animal husbandry. It usually causes little harm to the hunting industry, especially in the period of mass reproduction of mouse-like rodents, on which it mainly feeds. In those years with low populations of small rodents, does it sometimes attack large birds and hares. When populations are high, it may hunt the yellow ground squirrels and marmots; therefore in regions where these animals live, the number of corsac fox ought to be limited. In some regions, the corsac fox damages the hunting industry, eating animals that have fallen into traps, or dragging them off. Thus, in the Esil'sk region of Severo-Kazakhstan district, in the season of 1936/37, corsac foxes ruined 300 polecats which were taken in traps (Sludskii, 1939).

In a series of republics and districts, the corsac fox is protected as a valuable fur-bearer. Thus, it is completely forbidden to dig them out of burrows, smoke them out or drowned them. In the majority of republics, hunting this animal is only permitted in the season when it has prime fur—usually in November–March. In other times of year, the season is closed.

The Standard of Fur Raw Materials divides the untanned skin of corsac fox into four types according to the region where they were obtained and quality of the fur: Petropavlovsk, Kazakhstan, Astrakhan and Tashkent, of which the first type is the best and the latter is the poorest.

In periods when populations of this animal fell catastrophically, harvest was completely prohibited for many years over large territories. For example, in the majority of the regions of Kazakhstan, hunting of corsac foxes was prohibited from 1928 to 1938.

Hunting was permitted only in seven regions where a ground squirrel-gerbil industry existed (Irgizsk, Turgaisk, Karsakpaisk and others). Harvest of corsac fox was prohibited until 1939–1942 in districts north of Kazakhstan, for example, in Orenburg district from 1932 to 1939. This prohibition together with other factors favored the restoration of the corsac fox population. In the gerbil, marmot and other game industries, corsac fox populations ought to be restricted, without, however, destroying them completely. (A.S.)

*Local names of different trap types—Sci. Ed.

Fox, Vixen, Red Fox¹⁶

Vulpes vulpes Linnaeus, 1758

1758. *Canis vulpes*. Linnaeus. Syst. Naturae, ed. X, 1, p. 40. Uppsala, Sweden.
1758. *Canis alopex*. Linnaeus. Ibidem, p. 40. Uppsala, Sweden.
1777. *Canis caragan*.* Erxleben. Syst. Regni Anim. Mammalia, p. 566. Area of the lower Irgiz and Turgai [rivers] north of the Aral Sea.¹⁷
- 319 1789. *Canis crucigera*. Bechstein. Gemeinn. Nat. Deutschlands, 1, p. 250. Thuringia.
1811. *Canis melanotus*. Pallas. Zoographia Rosso-Asiat., 1, p. 44. Kazakhstan south of Orenburg (V.H.).
1816. *Vulpes vulgaris*. Oken. Lehrb. d. Naturg., 3, Th. 2, p. 1034.
1836. *Canis vulpes montana*. Pearson. Journ. Asiat. Soc. Bengal, 5, p. 313. Himalaya.
1843. *Vulpes flavescens*. Gray. Ann. Mag. Nat. Hist., 11, p. 118. Northern Iran.
1854. *Vulpes pusilla*. Blyth. Ibidem, p. 729. Salt range, Punjab.
1854. *Vulpes leucopus*. Blyth. Ibidem, p. 729. Mal'tan (Multan), Punjab.
1875. (*Canis vulpes*) var. *beringiana*. Middendorf. Übersicht d. Natur Nord- und Ost-Sibiriens, 4, Th.2, 1 Lief. p. 990. Asiatic coast of Bering Strait (V.H.) ("an den West-als an den Ost-Kusten des Berings-Armes").

¹⁶Hunters often call the male "*lisovin*".

¹⁷Erxleben (1777) stated that this form inhabited the "Kalmytsk and Kirgiz deserts", i.e. steppes, referring to it in two places in Vol. 1 of Pallas "Reise" (1811). The first reference (pp. 199–200) regarding the area south of the Samara river, is not precisely determined and may not require attention. The second (p. 234) refers to the area south of Orenburg where "the Kirgizes bring the steppe foxes (karagan) which do not differ in color from wolves" to be sold in Orenburg (and hence the diagnosis of Erxleben—"colore griseo-lupino"). The above mentioned type locality of the subspecies represents a more precise definition to references based on the usually cited type localities ("Kalmytsk and Kirghizian steppes", "Kirghizian steppes", "Kazakhstan") which are extremely broad. Karagans are, apparently, quite characteristic of the suggested limits of the type locality. Erxleben (1777) considered the karagan as "a doubtful animal" (animal subobscure). Later, Pallas (1811) considered it to have the status of a separate species differentiated from the red fox.

*Sometimes spelled *karagan*—Sci. Ed.

1902. *Vulpes vulpes splendens*. Thomas. Ann. Mag. Nat. Hist., 10, p. 489. Astrabad, northern Iran.
1903. *Vulpes anadyrensis*. J. Allen. Bull. Am. Mus. Nat. Hist., 19, p. 167. Markovo on the Anadyr [river].
1905. *Vulpes alpherakyi*. Satunin. Izv. Kavkazsk. Muzeya, 2, No. 1, p. 146. Geok-Tapa. Areshsk Co., Elizavetopol'sk Gub. [governance].
1905. *Vulpes kurdistanica*. Satunin. Ibidem, p. 48. Gel'sk depression, form. Karssk district, Turkey.
1907. *Vulpes vulpes tarimensis*. Matschie. Wiss. Ergebn. Filchner Exped. nach China, 10, T.1, p. 164. Tarim.
1907. *Vulpes vulpes tschiliensis*. Matschie. Ibidem, p. 169. Beijing.
1911. *Vulpes vulpes septentrionalis*. Brass. Aus. dem Reiche der Pelze, p. 454. Norway.
1911. *Vulpes kamtschadensis*. Brass. Ibidem, p. 456. Kamchatka.
1912. *Vulpes vulpes flavescens* var. *cinerascens*. Birula. Ezhegodn. Zool. Muzeya Akad. nauk, 17, p. 254. Eastern Khorassan, Iran.
1914. *Vulpes alopex* var. *caucasica*. Dinnik. Zapiski Kavk. otd. Russk. geogr. Obshch., 26. Zveri Kavkaza [Animals of the Caucasus], 2, p. 449. Vladikavkaz (after Ognev, 1926).
1914. *Vulpes vulpes krymea montana**. Brauner. Zapiski Novoross. Obshch. estestvoisp., 40, p. 15. Montane Crimea.
1914. *Vulpes vulpes crymensis*. Brauner. Ibidem, p. 36. Montane Crimea.
1914. *Vulpes vulpes crucigera* n. *stepensis*. Brauner. Ibidem, p. 15. Steppes between the Dnepr and Don [rivers], more exactly—Askaniya-Nova (V.H.).¹⁸
1922. *Vulpes alopex* var. *kamtschatica*. Dybowski. Archiw Tow. Nauk. Lwowe, 1, p. 350. Kamchatka. Nomen nudum.
1922. *Vulpes alopex* var. *sibiricus*. Dybowski. Ibidem, p. 350. Nomen nudum.
1922. *Vulpes alopex* var. *ussuriensis*. Dybowski. Ibidem, p. 350. Nomen nudum.
- 320 1922. *Vulpes vulpes jacutensis*. Ognev. Biologicheskie izvestiya, 1, p. 116. Vic. of Yakutsk.

*Sometimes spelled *krimeamontana*—Sci. Ed.

¹⁸Vicinity of Kherson, after Ognev, 1926.

1923. *Vulpes huli*. Sowerby.* Naturalist in Manchuria, 2, p. 44. Manchuria.
1924. *Vulpes vulpes crucigera diluta*. Ognev et Vorobiev. Fauna pozvonochn. Voron. gub. p. 102, Rocky steppe. Bobrovsk u[ezd] [county], Voronezhsk. Gub. [governance].
1924. *Vulpes vulpes schrenkii*. Kishida. Mon. Jap. Mammals, p. 41. Sakhalin.
1924. *Vulpes vulpes splendidissima*. Kishida. Ibidem, p. 47. Northern and middle Kuril Islands.
1926. *Vulpes vulpes alticola* Ognev. Uchen. zap. Severo-kavk. inst. kraevedeniya, 1, p. 52. Lake Gokcha (Sevan), Armenia.
- 1926¹⁹. *Vulpes vulpes karagan natio ferganensis*. Ognev. Annales Musei Nat. Hungarici, 23, p. 222. Osh, Fergana.
1926. *Vulpes vulpes karagan natio pamirensis* Ognev. Ibidem, p. 222. Near Pamir Post, Pamirs.
1926. *Vulpes vulpes ochroxantha* Ognev. Ibidem, p. 225. Aksai, Tien Shan.
1926. *Vulpes vulpes tobolica* Ognev. Ibidem, p. 227. Obdorsk, lower Ob' [river].
1926. *Vulpes dolichocrania* Ognev. Ibidem, p. 232. Sidemi in southern Ussuri territory.
1929. *Vulpes vulpes kiyomassai* Kishida et Mori. Lansania, 1, p. 82. Northeastern Korea.
1931. *Vulpes vulpes daurica* Ognev. Zveri Vost. Evropy i Sev. Asii, 2, p. 331. Kharagoi, 45 km west of Troitskosavsk (Kyakhta), Trans-Baikaliya (V.H.).

Diagnosis

Measurements large—body length more than 65 cm, greatest length of skull more than 115 mm. General color from light-reddish to grayish-ochre, brown; dorsal side of ear black, tip of tail white (V.H.).

*In original text, misspelled "Sowerdy"—Sci. Ed.

¹⁹Issued in the beginning of 1927 (April; V.H.).

Description

The red fox is a very well-formed, beautiful animal with an elongated body on relatively short limbs. The tail is long (longer than half the body length), fluffy, and in the standing animal reaches the ground. The muzzle is quite long and pointed.

In its short summer coat, the red fox appears lean with relatively long limbs, with a thin elongated body, large head and large erect ears broad at the base and pointed at the tips. Northern foxes, in their fluffy winter coat, look stocky with short limbs, massive body and a proportionally moderate-size head. The ears, the basal portion of which are hidden in the fur, are more proportional [appear smaller], the tail is especially long and fluffy, its overall length with hairs is nearly equal to the body length.²⁰ Southern forms of red foxes, in which the winter fur is relatively short, appear in winter as longer legged and “leaner”, their ears are larger—taller, and broader at the base.

Pupil of the eye is oval, and vertically oriented. There are three pairs of teats.

The winter pelage of the red fox is dense, soft, silky and relatively long. However, in connection with its very wide distribution and its occurrence under extremely different climatic conditions—from tundra to hot deserts—the geographical variation in this character is very great. In the northern forms, the fur is very long, dense and fluffy, while in the southern—much shorter, sparser and coarser (see section on “Geographic Variation”).

Still more variable is color of the winter fur of the red fox.²¹ This [variation] is especially complicated and great because, on a level with the well expressed geographic variation is wide individual variation. Besides form and amplitude of the latter, variation also is observed in types of morphisms. The picture is further complicated in that in various subspecies, not only is the extent of natural variability not the same, but also various color phases and types are encountered in various percentage ratios or are completely absent. For the latitude of variation in color and quality of fur, this species

²⁰Hunters very neatly call it “tube”.

²¹Color variation in summer fur was not studied, but judged by everything, it is less.



Fig. 117. Red fox, *Vulpes vulpes* L. Sketch by A.N. Komarov.

is divided into 41 sorts, most of which are in our animals. Within the sorts, they are separated into different color types. In addition, parallelism in geographic and individual variation is well exhibited in red foxes. Therefore, the red fox is one of the most variable in color of the species of our fauna. Notwithstanding that, variation in this species is realized through consistent geographic rules.

Two main geographic color types exist—northern red fox and the southern gray desert fox. To each of these types several subspecies belong. The extreme forms of both color types differ greatly from each other (Kamchatkan red fox—Turkmeniyan red fox), but they are connected to each other by a chain of gradual transitions through the characters of individual races, mainly those which occupy intermediate geographic positions, as well as through the individual variations within the limits of some subspecies which are mixed, in a geographic and systematic sense. The pelage of middle Russian and Turkmeniyan red foxes serve as examples of the geographic coloration of the first type.

Winter pelage of the middle Russian (around Moscow) red fox. General color bright reddish-rusty with yellowish tint. Along the spine, weak, diffuse pattern of many brown-reddish-chestnut

322 hairs noticeable; from this area, two diffuse stripes pass downwards to shoulder-blade. Together with spinal stripe, they form a striking pattern resembling a cross. In the posterior part of the back there are often some white or white-tipped hairs, giving the color in this region a mottled silvery appearance. The sides of the body are paler than the back; the side of neck is similarly colored. Chin, lower lips, throat and anterior part of chest white. The remaining lower surface of body dark, brown or reddish; sometimes a white stripe extends from chest to anterior part of abdomen. Greater part of groin dirty white, sometimes almost white, usually with one or another intensive reddish tint. Posterior part of thighs light and whitish. Sometimes, the color of the belly and inguinal region does not differ from that of the sides or even the back. Upper parts of limbs rusty-reddish. Anterior side of forelimbs, including forepaws, and paws of hind limbs, black anteriorly.

Anterior part of muzzle, forehead, vicinity of eyes, area between ears, and upper neck bright brownish-rusty-red. Upper lips white. On sides of muzzle anterior to eyes, no dark field, or only a slight darkening (browning) in form of a spot or stripe, passing from eye to region of vibrissae. Ears, from behind entirely black, or only the base has a brownish-reddish color similar in color to top of head. Inner surface of ear covered with whitish hairs.

Tail dorsally brownish-reddish, but less bright than back and side. Along sides and ventrally, it is pale gray with straw-colored tint. Many of the hairs, especially dorsally, have dark tips and hence a more or less intensive, blackish frosting. Sometimes, tail is intensively covered with black, and reddish tones are not developed. Along tail dorsally, slightly behind the base, usually a dark spot located in region of supracaudal gland.^{22*} Extreme tip of tail white, although size of this "flower" is variable.

Foxes of the type described are, in hunting terminology, usually called "*belodushka*" [white breasted] or "*berezovik*" [brown mushroom]. This is a certain modest type of fluctuating variability: animals duller and paler in their general tone are encountered, as

²²In a freshly killed animal, this gland, especially in freezing weather, gives off the odor of violet. This odor is not strong and rapidly disappears especially in a dead animal taken into a warm location. This explains why the presence of the "violet" odor is sometimes negated.

*Also called violaceous gland—Sci. Ed.

are others that are brighter. Especially bright and color-saturated animals are called “*ognevka*”²³ [fire].

Particular variations in *belodushka* lie in the distribution and greater or lesser intensity of the black color on the limbs, in reddening of the white area of the thoracic region and lightening (whitening) of the belly and inguinal regions, etc. Sometimes, the cross on the back is slightly darker than that described, and is revealed more clearly.

The other color types of Middle Russian foxes generally represent stages on the course toward melanism. These mutant color phase types are often, apparently, hybrids of the normal color type with melanistic mutants. Melanism in the form of a light admixture of black pigment appears also in foxes that are in all respects true “red” type. Sometimes, it is particularly obvious—it is the “mediocre” of furriers. Three types of true, more or less sharply separated, melanists are differentiated.

Sivodushka [gray breasted]. “Rump and spine brown or gray color with more or less marked zonation of guard hairs; light bands of these hairs not white, but yellowish. Underfur on rump and spine gray, without light tips. Cross on shoulders brown, rusty-brown or brownish-reddish. Part of fur along sides of this cross are reddish or yellow color. Sides with large admixture of yellow or reddish guard hairs. Chest and belly dark brown, sometimes with white spot in center of chest. Limbs brown”.

Krestovka [cross fox]. “Fur has darker coloration. Rump and posterior part of spine dark brown or dark gray in color with more or less well developed silvery color (white zones) on guard hairs; underfur in these parts of the skin dark gray throughout whole length of hair. Cross on shoulders black or blackish-brown, sometimes light silvery. Parts of fur at corners of this cross are golden yellow or rusty. Admixture of yellow or reddish hairs usually also obvious on anterior part of sides of skin. Chest and belly dark brown (on chest, a white star sometimes appears). Feet and head brown”.²⁴ In some places, hunters call red foxes, but with a more

²³This terminology of Middle Russian hunters does not fully coincide with the terminology of furriers (see below), especially the term “*ognevka*”.

²⁴According to Kuznetsov, 1952. In furriers terms, the chest is called *dushka*, the belly—*cherev*, and the rump—*oguzko*. The characters mentioned are standard characteristics.

sharply marked cross-like pattern, a "cross fox"; which is, however, not black or black-brown, but only a somewhat darker tone than the general fur color. In exactly the same way, sometimes forms only somewhat darker below are called gray-breasted, but they actually are only a transition from the red fox to the true *sivodushka*, etc.

Chernoburaya [blackish-brown]. The whole skin is blackish-brown, or black with light brownish tint. Usually, the skin has a admixture of various amounts of "silver", i.e. pure white guard hairs or black guard hairs with a white zone. Reddish hairs are completely absent, or they are found in small quantities.²⁵

Between all of these color types—from the *ognevka* [fire] to the *chernoburaya* [blackish-brown], there is a more or less complete chain of transitions. Moreover, in one litter may be encountered both red, and also melanistic, foxes (Hofman, 1856; Middendorf, 1869; Maidel, 1894; Iokhel'son 1898; Sokol'nikov, 1927; Folitarek and Chirkova, 1930).

Melanism in foxes is, to a significant degree, geographically localized. Melanists are more often met with in the forest zone and in the forest-tundra belt, especially in middle and eastern Siberia, and also in the Caucasus mountains. In Taimyr, in individual years, *sivodushka*, *krestovka* and *chernoburaya* occurred in up to 20–30% of the prepared skins. Melanism is manifested also in other natural zones, being, however, very rare in steppes and deserts (Pallas, 1788; Kessler, 1850; Eversmann, 1850; Chernai, 1853; Bogdanov, 1871; Karelin, 1883; Alferaki, 1891). Appearance of melanists in one or another place changes yearly. In years of fox abundance, the relative quantity of melanists increases and in the years with low number, decreases (A.F. Chirkova). In Canada, the number of melanists found is proportional to the abundance of red foxes (Hewitt, 1921).

²⁵The "black-brown fox" described as is clear from the above is a wild melanistic form of the Eurasian red fox. That which ordinarily was usually called black-brown fox or in vulgar form, "*chernoburka*," is the so-called "*chernoser-ebriстая*" [silvery black] domestic fox, raised in captivity, the melanistic form of the American red fox. It is characterized by pure black color with a variable admixture of silvery (from 25% to 100% of the skin area). Selection of this form proceeded by eliminating the brown and establishing in the pelage a pure black tone of the skin. Brown is considered a defect which lowers its value.

The described dark forms of foxes are distinguished by the exceptional beauty and uniqueness of the fur and are valued very highly (due also to their rarity). Usually (this partially depends upon fashion) *krestovka* are valued more highly than *sivodushka*, and *chernoburaya*—higher than *krestovka*.

Depigmentation of the pelage and complete or partial albinism (if limbs are white, then foxes are “in white stockings”) seldom appears among foxes (especially complete albinism). Known cases
 324 of albino foxes more often appear in the southern forest zone, but they are also encountered in other natural zones (Krasheninnikov, 1755; Eversmann, 1850; Rossikov, 1887; A.M. Nikol'skii, 1889; Slyunin, 1900; Dinnik, 1914; Pomerantsev, 1939; Dvoichenko, 1955; Korneev, 1956 and others). Albinism, along with several deformations, usually develops in foxes after years of insufficient food (A.F. Chirkova). Chromists appear even more rarely, for example, red foxes without a white “*dushka*” [breast], etc.

Summer fur in all formed of red foxes is short, sparse and coarse. Generally, it has the same color as in winter, but is duller, dirtier and less bright.

The young fox in the first coat has short, dense wool dark blackish-brown in color. The lower part of the body is somewhat grayer, but it is almost undifferentiated from the upper part. On the forehead above the eyes, there is sometimes a frosting of rusty tone; on the chest, a small white spot often occurs. The extreme tip of the tail is white. The replacement of this coat by the second begins very quickly, in which the reddish tone is well developed. This is the first adult coat. There is no sexual dimorphism in color.

Winter pelage of the gray desert (Turkmenian) fox. The distribution of the areas of various color intensities is generally the same as described in the red fox, but reddish color tones are absent, or in place of them, only light sandy yellow. Dull-yellowish or gray general tone of fur predominates. Head yellowish-creamy or sandy in color, with more intense color on forehead and upper part; muzzle whitish. On muzzle, in front of eyes, there is a well defined dark spot or band passing from eye to region of vibrissae, colored dark gray, reddish-brown or blackish-brown. Sometimes they are weakly developed. Greatest part of rear surface of ear pure black or brownish-black. On upper neck and back, color more intense, and yellow or brownish tones more evident in it; it extends over the shoulders also, forming a cross-like figure. On posterior part of

body, dorsal stripe more strongly speckled with light-whitish and light-yellow hairs. Sides gray, without a yellow admixture or with very weak dilution of this tone and in general is brighter than back. Along whole body, there is a mixture of black or brown guard hairs, forming evenly spaced light and dark dappling.

Throat white, chest and belly whitish or gray, chest often being gray. Feet gray without black stripes, or else an ill-defined darkening present. Color of inner parts of feet yellowish. Tail light gray-whitish dirty tone. On upper surface near base (in region of supracaudal gland), is found an ill defined blackish or grayish spot. Mixture of black hairs along whole tail, more abundant on sides and on lower surface.

The normal (fluctuating) color variation in foxes of this type is not less, and in some places, even more than in red foxes. For example, just in the neighborhood of Ashkhabad, seven color types are well marked (V.G. Heptner). Among them are encountered all varieties from pure gray and even fairly dark gray animals to those in which yellow tones are well developed (all skins appear bright yellow) and, as a really rare exception, foxes with quite bright yellowish-reddish color. The lower surface of the body may be white, or sometimes even brown. The cross is also subjected to variations. Deviations towards reddish color are, however, more rarely met with than towards grayish.

Variations in the form of *sivodushka*, *krestovka* and *chernoburaya* among gray foxes are encountered more rarely than among the red foxes, and in some territories they are completely absent.

The summer fur is very short, sparse and coarse; it is characterized by predominance of gray tones, but well developed ochre occurs.

- 325 The fox skull is fairly narrow and elongated, with a small braincase and relatively narrow, more or less rounded, zygomatic arches. In the region of the infraorbital foramen, the skull looks somewhat compressed, and the line of the zygomatic arches passes fairly abruptly into the outline of the rostral region. Rostral part of skull quite long and attenuated: distance from posterior margin of infraorbital foramen to posterior margin of canine alveolus greater than skull width above canines. Ratio between length of nasal bone and that of distance from their posterior margin to most prominent point of occipital region comprises 1 : 1.2–1.5.

Line of upper profile not straight—there is an evident depression in region anterior to preorbital foramen and forms quite convex line in fronto-parietal region. Braincase relatively narrow and elongated posteriorly—posterior border extends significantly backwards behind line uniting articular condyles of lower jaw. In small southern forms, braincase somewhat larger relatively and more swollen than in northern forms. Well defined groove runs from level of supraorbital processes along suture between frontal and nasal bones.

Occipital crest well developed; sagittal crest quite well developed in some forms (large northern foxes) and in others (small southern forms)—very weakly. In first, temporal lines pass back from postorbital processes at acute angle in respect to each other. They enclose a small, narrow triangular area and pass to arrow-shaped crest at level of, or immediately behind coronal suture (in old individuals). In small Middle Asiatic forms, temporal lines run almost parallel, outlining a quite large area, and then diverge, joining small arrow-shaped crest near occipital (here, one of the evident “infantile” characters of the small southern form of fox is shown, both in development of crests and structure of braincase itself). Ends of paroccipital processes located only slightly lower than level of lower margin of auditory foramen. Length of symphysis of lower jaw 4–5 times shorter than greatest length of entire mandible.

Canines relatively long: when jaws are closed, lower extend beyond edge of upper alveoli; ends of upper canines (if skull is viewed from in front) extend below lower border of anterior part of lower jaw.

Individual variation in skull quite significant not only in general dimensions, but also in proportions. Skull within limits of species norms, may be relatively short and wide, or narrow and long (elongated). Description of a separate “species”—*V. dolichocrania* (Ognev, 1926)—was based on a specimen with an extreme degree of dolichocephaly.

Sexual differences in the skull are expressed in smaller average size of the female skull, and this difference is more pronounced than in corsac fox. As a group, females have, apparently, a somewhat wider nasal region and hard palate, canines are somewhat larger and the upper tooth row is longer (Ognev, 1931). However, these characters require verification. Apparently, females have somewhat weaker skull sculpturing.

Age variation in the skull proceeds, in the direction of growth in the relative size of the facial region and decrease in that of cranial region and relative decrease in size of braincase. The oldest animals have skulls with especially elongated facial parts, relatively small braincase, and well developed temporal lines and crests. Several proportions and structural characteristics of the skull exhibit geographic variation (see beyond).

The diploid number of chromosomes is 38.

Dimensions of the fox exhibit significant age, sexual and individual variations. Moreover, geographic variation is also great. At the same time, up to the present there is little accurate information
327 on body dimensions and weight of the animals; data concerning skull size are considerably greater.

Body length of adults is 49–90 cm, tail length without terminal hairs—53–60 cm, ear length—7.7–12.5 cm, length of hind foot is 12–18.5 cm. Height at shoulder is 35–50 cm.

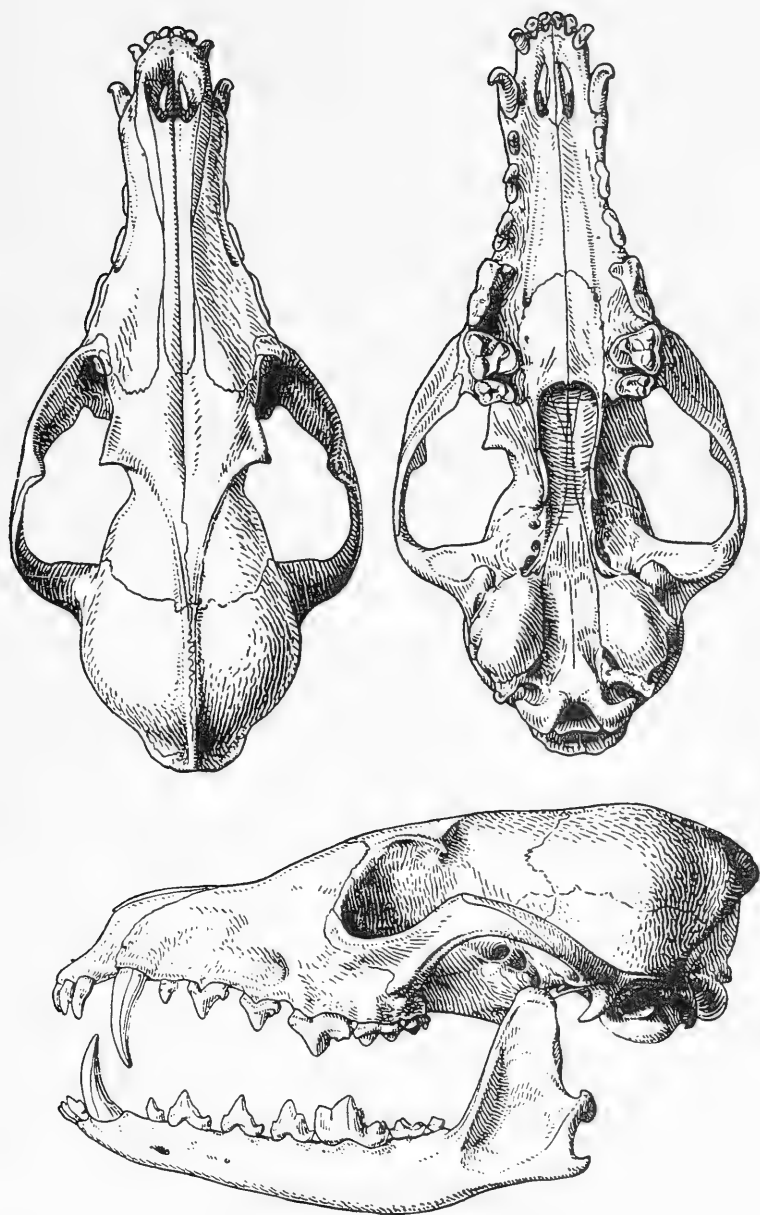
Weight is 2.2–10 kg. Females are somewhat smaller and lighter than males; in each locality, their weight is approximately 15–20% less.

Maximum skull length of males is 129–167 mm, females, 128–159 mm; condylobasal length of skull in males is 125–160 mm, females, 115–145 mm; zygomatic width in males is 64–89 mm, females—61–83 mm; cranial width in males is 41–52 mm, females—41–51 mm; length of upper tooth row in males is 60–70 mm, females, 52–69 mm.²⁶

Systematic Position

Apparently, the red fox must be considered a more specialized species than the above-described *V. cana* and *V. corsac*, as well as *V. bengalensis*. In any event, the skull of *V. vulpes*, even the smallest forms, possesses fewer infantile features than the skull of the mentioned species. The great development of the facial part of the skull must be considered a large specialization in the direction of carnivory. The large size of *V. vulpes* may also be considered as a progressive feature. Characteristically the southernmost forms

²⁶The figures given relate only to adult animals, but are attributed to the species as a whole (within the USSR)—data on separate subspecies are given in the section “Geographic Variation” (V.H.).



of *V. vulpes* (*griffithi*, *pusilla*, from ours—*flavescens*), as compared to the northern ones, have more primitive features of the infantile type—the relative development of the facial region, development of crests and several others. In a certain sense, they show transitional features from *V. vulpes* to the above-mentioned small species.

Nevertheless, within the genus *Vulpes*, s. str. *V. vulpes* must not be considered the final link. The Tibetan *V. ferrilata* represents a species which is still more specialised, in the mentioned trends, than *V. vulpes*. This is a higher manifestation of the fox type.

The North American red fox is identical with our fox in regards to species, although the American authors considered it up till now, a separate species—*V. fulva* Desm., 1820 (Hall and Kelson, 1959). Specific identity of both species is apparent not only from their morphological characteristics, but also their zoogeographic relationships. Both forms can be freely crossed in captivity and yield normally fertile offspring. Probably, this also occurs in nature. In any event, the European red foxes brought into the eastern part of the United States are indistinguishably mixed together²⁷ (V.H.).

Geographic Distribution

328 The range of the species is very vast, and occupies the Old World from the Arctic Ocean southward to North Africa, Arabia, northern India and northern Indochina. In the New World, the range extends from the north of the continent to the northern shore of the Gulf of Mexico.

²⁷The most recent information on this question is as follows: "Red foxes (*Vulpes vulpes*) were introduced numerous times from England between 1650 and 1750, and may have become naturalized or crossed with our native red foxes (*V. fulva*). The survey did not contribute any new information on the debatable question of whether present fox populations of the east-central and southeastern states are entirely native, a mixture of native and introduced animals, or entirely from introduced animals, as deduced by Gilmore (1946)" (Presnall, 1958).

"Whether the red fox of the eastern United States (much or all of the area shown, on the distribution map as the range of *Vulpes fulva fulva*) is a native animal or instead a stock introduced from Europe is unknown at this writing" (Hall and Kelson, 1959).

Geographic Range in the Soviet Union

This comprises a very large part of the species' range, and covers the entire state territory except the very far north.

The northern border includes the whole of the Kola peninsula together with neighboring islands (Kil'din), Solovets islands, Kanin peninsula, Kolguev Island, Vaigach and Yuzhnyi islands of Novaya Zemlya—along the western coast to Gusinaya Zemlya inclusive. In Yamal, the border passes through the region of crooked-forests [krummholz] (forest-tundra), approximately along the Khadyt river. Farther east, it coincides with the sea coast of the Ob' Gulf and extends to the mouth of the Taz. Hence, the line of the border, apparently bypassing the Gydansk peninsula, suddenly ascends to the northeast, crosses the mouth of the Yenisei in the northern part of Brekhovsk islands (red fox normally occurs around Dudinka), passes on to the lower course of the Pyasina, where it reaches 73° N. Lat. (mouth of its left tributary, the Kura).

In Taimyr, the northern border of the range ascends to the latitude of Lake Taimyr (about 74° N. Lat.; E.I. Shereshevskii), whence it descends to the mouth of the Khatanga, including its large left tributaries, the Balakhna and Gusikha (to 70°30' N. Lat.). Farther to the east, the fox is met with along the lower Lena (occurs around Bulun), and in the Lena delta and along the shore to the east (Tiksi, Cape Bykovsk—72° N. Lat.). From the Yana to the Indigirka, the border coincides with the coast of the Arctic Ocean and, apparently, runs even to the Bering Strait itself. The eastern border of the range consists of the Pacific Ocean. The fox lives on Karaginsk Island, on all of the Kurils (except the very smallest), on Sakhalin and Shantar islands; on the Commander islands they are absent.

The border as indicated is approximate to a certain extent. The northern border of permanent denning of the fox is quite well defined by the northern border of the forest-tundra, although in open tundra, the animal also reproduces in some places, sometimes even quite far to the north (Kanin). However, this rarely occurs. At the same time, the fox penetrates the tundra, especially in the south, very often. Therefore, it is difficult to determine the northern limits of the regions of settlement and of transgressions. Foxes pass especially far to the north along river valleys overgrown with arborescent and shrubby vegetation far beyond the limits of forest-tundra.

Apparently, Vaigach and Novaya Zemlya especially represent regions of transgressions by the fox as well as extreme northern points in eastern Taimyr. As well as short-distance dispersal, at some places very distant ones occur. Thus, in Yamal, a fox was observed in the tundra area, even to Cape Drovnyani (northern termination of the peninsula), and in western Taimyr, nearly to Dikson (Slobodsk Bay). Transgressions of the fox on to the Lyakhovsk islands are known, particularly to Bolshoi Lyakhovsk, on the ice of the Chukotsk Sea 100 km from the continent, and even to Wrangel' Island. In the latter case, the animal must have traveled not less than 150 km²⁸ across the ice. These transgressions are, of course, extremely rare. Thus, on Bolshoi Lyakhovsk, only 2 foxes were caught in a period of several years. During this same period, 5,500 Arctic foxes were captured (E.I. Shereshevskii).

Geographic Range outside the Soviet Union

This includes all of Europe, northward to North Cape, on the west including Ireland, southward to Sardinia, Corsica, Sicily and Cyprus; in Africa—lower Egypt, the Fayum, Libya, Tunisia, Algeria, Morocco, Rio-de-Oro and Senegal. In Asia, the range includes Asia Minor, the entire Arabian Peninsula, Iraq, Iran, Baluchistan, Afghanistan and all of Central and Eastern Asia, to the south including Kashmir, Punjab, Sind, Kutch, Kumaon, the Himalayas (including Sikkim), south China (Fujian, Yunnan) and Bakbo (Tonkin Gulf) in North Vietnam, and also the Japanese islands.

331 In America, the range includes the continent on the north to the Arctic coast, and the coast of the Bering Sea. The southern border of the range is complicated. To the east of the 90th meridian, it reaches the Gulf of Mexico; however, foxes are absent in Florida and in the eastern parts of Georgia and North and South Carolina. To the west of the indicated meridian, the fox is absent in a vast area extending in a north to south belt from Texas, Oklahoma, and New Mexico in the south to the southern part of Saskatchewan and Alberta.* It is also absent in a narrow strip along the Pacific coast, beginning on the Kenai Peninsula, and in parts of California,

²⁸Range according to data of Vrangeli, 1841; Middendorf, 1860, 1869, 1875; Zhitkov and Buturlin, 1901; Zhitkov, 1904, 1913; S. Naumov, 1931; Ognev, 1931; Adlerberg, 1935; Kolyushev, 1936; Mineev, 1936; Portenko, 1941; Novikov, 1956; Heptner, 1936 and others and according to unpublished material of E.I. Shereshevskii.

*The red fox is now present in most of this area—Sci. Ed.

Nevada, Utah, Oregon and Idaho. The southernmost limits of fox distribution in America, starting from the west, lie in California, Arizona, New Mexico, Texas and Louisiana (from Hall and Kelson, 1959).

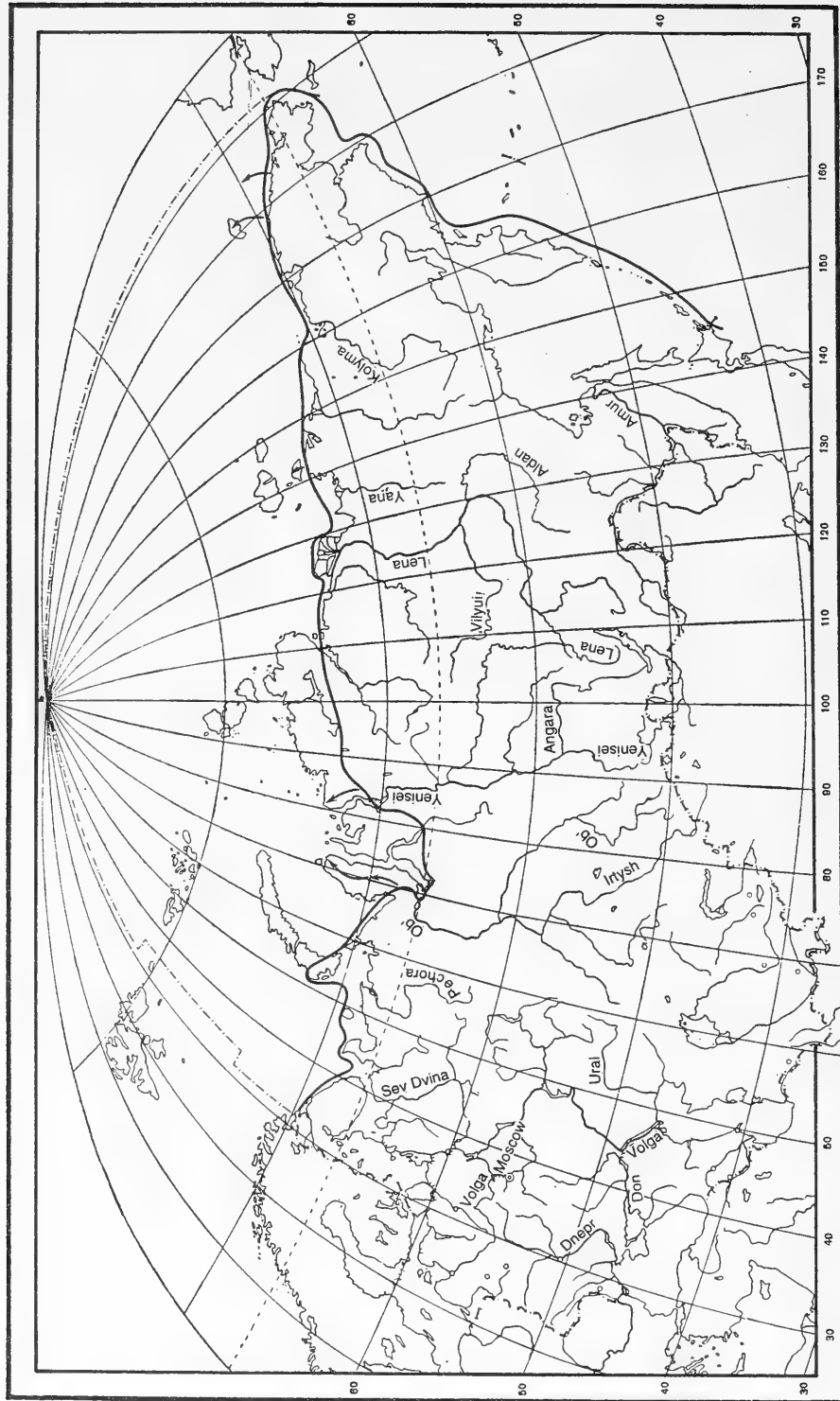
On the American Arctic archipelago, there are no red foxes, but they are found in Newfoundland, islands of the Gulf of Saint Lawrence, and on the Atlantic coast, and on Kodiak and Saint Lawrence islands in the west. It is absent on other islands of the Bering Sea and Pacific Ocean.

The European red fox has been acclimatized in Australia and inhabits nearly all of that continent, and the European (English) form was imported into North America (see above) (V.H.).

Geographic Variation

Geographic variation in the red fox is very great. It is greater than in all of our other carnivores, and greater than usually occurs in mammals of that size, and with similar biology. This concerns not only the number of geographic races which it forms, but also the amplitude of geographic variation in morphology. This is related to its broad range, and occupation of very diverse natural situations and entirely variable biotopic relationships. Thus, if the fox of the northern taiga lives with a winter lasting 7–8 months, with bitter cold and deep snow, then the animals of southern Turkmeniya basically do not know true snow cover, but live with severe heat and moisture deficit for almost half the year. There are as many sharp differences in nutrition as well. A large role in the wide geographic variation of the red fox is played by its extreme general plasticity, including individual variation. This is greater than in other, just as widely distributed, species. Thus, individual and geographic variation in the wolf and other foxes cannot be compared with that of the red fox.

The picture of the geographic variation in red fox is very complicated and difficult to study. Changes are observed in general dimensions of body and skull, comparative measurements of some body parts (ear, tail), several particularities of skull structure (see above), particularities of pelage (see above), thickness of the skin (the hide itself) and lastly the color. If in the main all listed categories of features are “normal”, nonetheless some have individual variations of significant amplitude, and in the character of color



329 Fig. 119. Northern and eastern borders of the distribution area of the fox, *Vulpes vulpes* L. in USSR. Arrows show the direction and places of the especially long transgressions to the north (V.G. Heptner).

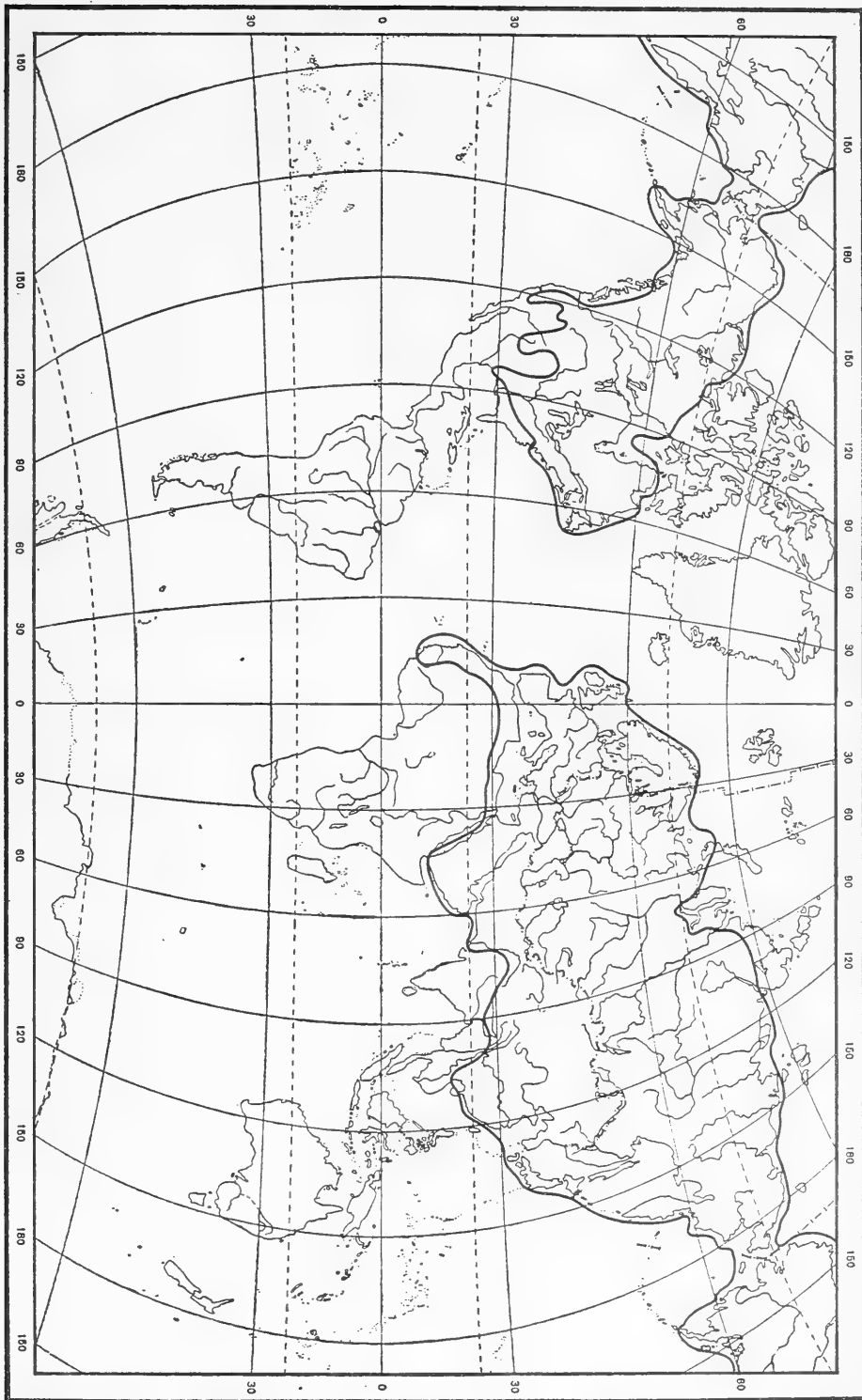


Fig. 120. Species range of the fox, *Vulpes vulpes* L. (without area of transgressions to the north) (V.G. Heptner).

greatly exceed the "normal" range in other species, even those which are highly variable in this respect. Practically every geographically limited, and in a systematic sense, homogeneous population has some more or less well differentiated types of individual variations of the basic ("normal") color phase. This concerns the general tone and intensiveness of color, the degree of manifestation of the dorsal stripe and shoulder stripes, foot color, color of the venter—chest and belly, the character of facial pattern, etc. These types are characterized by one of the features mentioned or a combination of them.

In individual variation in color of the different geographic populations the following particularities exist, important for an understanding of geographic variation in the species.

1. In various geographic populations (subspecies), the number of color types differs; more or less variable populations exist. Thus, in the population in the vicinity of Ashkhabad one may distinguish 7 types of individual color variations (V.G. Heptner). In others, 2, 3, or 4 color types are designated, so on.

332 2. The portion of each of these type is not identical, and equally with one, or one or two predominant ones, others are encountered more rarely, and the remaining are very rare. In general, there is usually a normal curve of distribution.

3. In various geographic populations, there are different types of individual variations. Thus, in the north there are no gray foxes, nor in the south *ognevka* [fire] (see below). The more distant geographically the populations are, the more they differ from each other in the set constituting their color types.

4. In populations, the set of color types which are more or less the same, may differ fundamentally in the percentage of different color types contained, and various color types may predominate; the prevailing color type of one may be rarer, or even rarer in another [color type]. In this way, each geographic population is characterized by: (a) its set of types of individual variations and (b) prevailing type (or types) of color.

5. These relationships become complicated, and general variability of the population greater, in regions where one defined form of the population (or subspecies) is contiguous with and mixes with another ("introgress with one another"), especially if several come together. This occurs, for example, in regions where vast flat lands are contiguous with mountains (eastern Trans-Caucasus).

6. Color type sets are especially varied, the relative percentages are especially complicated, and sharp variations in these relationships are seen in small areas in those countries where in relatively small areas, landscape-geographical, zoogeographical and ecological conditions and relationships change abruptly and are complicated, as for example in the Caucasus (see below, and detailed material concerning this question in Vereshchagin, 1960).

7. Geographic difference in the distribution of color phases (*sivodushka*, *krestovka*, *chernoburaya*) and their hybrids with the "normal" foxes are related to the variations of the "normal" color type. These phases, despite their scarcity, are found in some regions more often than in other regions, and in still other regions they are completely absent.

In the above-mentioned situations, geographic variation in the fox is manifested especially sharply, especially in color, and with an amplitude greater than in other characters.

As a result of extensive study of hundreds of thousands of skins of animals caught annually for the fur trade, 41 "*kryazh*"* of the normal color phase of fox are differentiated as regards color, fur quality and in part, size. In these types, which are characterized by one and sometimes two prevailing color types, geographic variation of the species is well manifested. However, there is no full coincidence between the types and subspecies. In many places, within the limits of a population belonging to one subspecies, prepared fur is assigned to several types depending upon the properties of the fur. Thus, in the vicinity of Ashkhabad, foxes are sorted into 2-3 types, and in various parts of Caucasus, where physical conditions are especially complicated, they are sorted into 2, 4, 5 and even 8 (Vereshchagin, 1960). Therefore, the type is characterized by both the actual geographic group, and by individual deviations. Usually only groups of types are coincident with geographical races (subspecies). A mixture of the types in some places is, apparently, connected with the fact that here is found an area of mixing and introgression, of entirely different geographical populations (subspecies) as regards the color. It may also be connected, to a certain degree, with hybridization.

An attempt is often made, especially by hunters, to relate the defined color types of foxes in a given limited place to ecological

*Lit., "blocks," or types—Sci. Ed.

variability ("reed", "steppe", "montane", "marine", "tundra" foxes, etc.). However, there is no foundation for this. Only in some
 333 places in the foothills or the base of the mountains, may montane and plains foxes actually be differentiated. But this is only in those cases when the plains are occupied by one subspecies, and the adjacent montane country—by another, and individuals of both subspecies are met with in a defined zone. Such a picture exists, apparently, in places in southern Tadzhikistan, where the plains are inhabited by *V. v. flavescens* and in the mountains of Pamir-Alai, *V. v. ferganensis* is distributed (Flerov, 1935; Chernyshev, 1958). The described complexity of color variation in the red fox makes the study of geographic variation in the species very difficult.

A series of described subspecies are unfounded, since they are separated on the basis of individual deviations. On the other hand, color characteristics actually present can only be established by a large series and in an entirely general form according to an average—the prevailing color type. The establishment of all amplitudes of variability in this feature is practically impossible at the present time.

In actuality, all geographically varying characters of red foxes do not develop irregularly and independently of one another, but are parallel and geographically regulated. In their development, several general rules of geographic variation are well revealed.

Northern foxes occupying the forest zone are the largest; also large are those of the forest-steppe and steppes of the European part of the Soviet Union, and the northern steppes of the Asiatic part of our country. Foxes of the southern steppes and semideserts are smaller, and animals of the extreme south—the deserts of Middle Asia—are the smallest; foxes of extreme southern Turkmeniya (Badkhyz) are particularly small. Foxes of southern Afghanistan, Pakistan and India are still smaller. In the south (Middle Asia and Trans-Caucasus), montane races of foxes are somewhat larger than those inhabiting the lowlands.

The average area of a fox skin in Bashkiria (Bashkirian sort) is 2,908 cm², that of foxes of the Middle Asian plains (smallest—Tashkent type)—1766 cm². The weight of 100 skins of Bashkirian fox is 40.5 kg on the average; that of Middle Asian plains—27 kg (Kuznetsov, 1952) (skin weight characterizes length and density of fur, but mainly general skin dimensions). Weight of Middle Russian (Moscow) foxes is 4–10 kg (Ognev, 1931); weight of foxes from

the plains of southern Tadzhikistan (right bank of Amu-Dar'ya) is 2.2–3.2 kg (Chernyshev, 1958). The large foxes of the forest-steppe zone of the European part of the Soviet Union have a body length up to 90 cm, averaging 72 cm; the foxes of southern Tadzhikistan are only 49–57.5 cm. The weight of a carcass without skin is in the first case usually 4.4–8 kg, and in the second, averages 2.7 kg (Chernyshev, 1958; A.F. Chirkova). Foxes of the steppes and semideserts of Asia and certain other intermediate regions (some parts of Caucasus) occupy a transitional position between these two extreme groups.

Skull size also very clearly decreases from north to south, reaching its minimum on the plains of Middle Asia, and especially in southern Turkmeniya. Condylbasal length of the skull of foxes of the upper Pechora (Pechoro-Ilychsk preserve) varies in males (28) from 131.5 to 158.9 mm, resulting in an average of 145.4 mm. Such dimensions, apparently, have foxes of the entire taiga zone, although larger individual populations occur. Thus, in the foxes of Kirov district (26), average condylbasal length of the skull is 149.6 mm. Foxes of Middle Russia and the northern steppes of the European part of the Soviet Union (Voronezh, Poltava) are similar to Pechora foxes. The smallest fox of the plains of Middle Asia (14, Ashkhabad) has a condylbasal length of adult male of 125.7–139.1 mm, on average 132.4 mm. In foxes from Kushka, this measurement in males is 129.9 mm and in females, 123.5 mm. Therefore, maximum size of the southern form is less than the average size of the northern form, and the average skull size of the smallest race constitutes about 88% of the larger. Skulls of foxes living still farther south (Indian, Pakistanian and southern Iranian forms—*griffithi*, *pusilla*) is still somewhat smaller. In the intermediate regions, there are populations of transitional character. In the south (Caucasus, Middle Asia), montane forms of foxes are usually somewhat larger than those of the plains. Bergman's rule is well exhibited by the described species.²⁹

Geographically oriented changes in qualitative skull characters exist. The skull of the northern fox has a relatively smaller cranium, and strongly developed crests; there is quite well developed sexual dimorphism in size. Small foxes of Middle Asian plains have a

²⁹Values in unpublished material of V.E. Yakob'. For foxes of the Tadzhikistan plains, the trend is toward even smaller values (minimum—115.1 mm. Chernyshev, 1958), but they belong, however, to specimens that are not fully mature.

relatively large cranium, and more weakly developed crests (see above and Fig. 121). On the whole, the skull of the southern fox possesses infantile features and, in connection with this, sexual dimorphism is relatively weak.

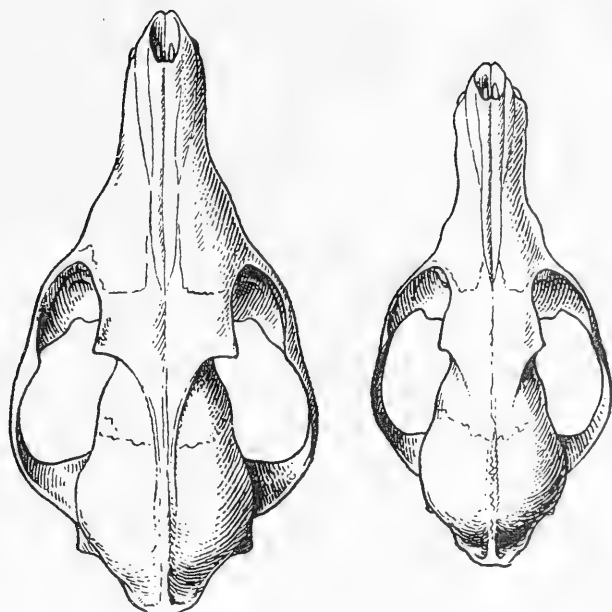
Variations in body proportions are expressed in that southern foxes possess a relatively longer tail and longer ears (Allen's rule). Montane subspecies in the south (Middle Asia, Caucasus) possess relatively shorter ears than plains forms at the same latitudes (A.F. Chirkova). Southern foxes have, apparently, somewhat longer limbs.

The length, fluffiness and softness of the fur varies regularly in the same manner (from north to south). Northern foxes have dense, long, soft and silky fur, the southern—sparser, shorter and coarser. In foxes of the Ob' lowlands (West Siberia), length of guard hair on the sacrum ("on the rump") on average equals 69 mm, that of underfur—52 mm. The same indices for foxes of the Middle Asian plains—48 and 35 mm, which constitute only 70% of the northern. The coefficient of softness of rump guard hairs in Yakutsk fox (especially soft hair) is equal to 1.3; while in the coarse-haired southern foxes (Caucasus), it registers 2.2 (Kuznetsov, 1952)³⁰. In the south (Caucasus, Middle Asia), montane subspecies of foxes have denser, longer and softer fur than plains forms in the same latitudes.

335 The thickness of the skin ("hide") significantly varies geographically. In northern foxes, it is thin, in foxes of the middle zone, of moderate thickness, and in southern, thick and rather rough. Thus, in Yakutsk fox, thickness of the skin ranges between 0.22 and 0.24 mm, with an average of 0.23 mm, while in the Kazakhstan—from 0.40 to 0.42 mm, with an average of 0.42 mm, i.e., it is nearly twice as thick (Kuznetsov, 1952).

Color for all of its variegation and variability, shows completely regular changes geographically. This is revealed in variation in the general intensity and saturation of color of the main types, and in the replacement of these main types when subordinate ones come to prevail, and similarly in changes of the set of color types themselves. Elements of the whole spectrum of color types have an amplitude from bright red-ginger to gray in some regions, as if successively displaced from one territory to another. At the same

³⁰Coefficient of softness is the ratio of the hair thickness in microns to its length in millimeters. The character of the skin can also be judged by skin weight, as given above.



334 Fig. 121. Skull of Middle Russian red fox (*V. v. vulpes* L.—on the left, Kirov district) and Turkmeniyan red fox (*V. v. flavescens* Gray, Turkmeniya, Repetek). Males with similar degree of tooth wear. Sketch by N.N. Kondakov from material of the Zoological Museum, Moscow University.

time, the role of each color type successively changes from null to predominance (and vice versa).

The brightest, most saturated reddish-ginger “*ognevka*” [fiery] color tones are in red foxes in the northern Far East, including Kamchatka and Yakutiya. They have almost no bright ripples on the spine and rump and the sides are brightly colored. On the anterior side of the foot, there are large, bright black spots. In these regions, the “*ognevka*” is evidently prevalent. In all of the remaining forest zone, the bright-reddish color is distributed, but is not the saturated hue of the “red fox” (as called by furriers). They have a well defined light, bright ripple on the thighs and in the posterior part of the spine. Sides are relatively light. On the feet are large well defined black spots.

In the forest-steppe districts of Siberia, in the steppes of the European part of the Soviet Union, i.e. south of the forest zone, and in the mountains of Middle Asia, lives the “crimson fox”, which is less intensive colored than the forest one. In them the spine and

cross on the shoulder are bright-reddish or rusty-yellow in color, the sides are sandy-yellow. The dark spots on the feet are small, narrow and dark-gray in color.

Farther to the south, in Kazakhstan and Middle Asia, the color of fox either becomes lighter or grayer. In the semideserts and deserts live "light" foxes in which the spine is a light-sandy color, usually with a lighter band, the sides are whitish and very light, and on the feet is a narrow band of dark-gray, and "grays", in which the spine and sides are gray in color, sometimes with weakly defined dull-reddish tones along the backbone. The foxes of the mentioned regions are usually known as *karaganka* [pea shrub foxes]. "Grays" represent the extreme degree in loss of reddish pigment. They predominate in the extreme south of our country. Between the districts occupied by foxes of the deserts ("light" and "gray") and the Asiatic forest steppe lives a population of a more or less intermediate character. In this way, a successive change in fox color from "fiery" to "gray"³¹ runs from the northeast of the continent to southern Turkmeniya.

A legible picture of pigment loss is also observed in the foxes of Caucasus, but it is very complicated. Here is encountered the "red-gray" fox, in which the spine and sides are of gray in color with a clearly defined rusty band along the backbone, and also the above-described "gray" fox, several types of red color with yellow tones; gray and red-gray foxes are mainly native to the plains of the Trans-Caucasus, and in part the Cis-Caucasus; the remainder are in the Cis-Caucasus and the montane parts of the country.³²

³¹On a plane with the above-mentioned main types, furriers, in separate places, differentiate other deviant or transitional types—light-red and dark-red, light-scarlet, light-yellow, scarlet-yellow, red-scarlet, brick-red, brownish-red, light-gray foxes, etc. Local hunters, nearly everywhere, in their turn distinguish various forms, mainly on the basis of color: in addition to above-mentioned forms, "*serebryanka*" [silvery], "red" "*berezovka*" [birch], "*belodushka*" (white chest), etc.

Characteristics of the color types of fox were mainly given according to Kuznetsov, 1952. Therein is presented also detailed data on fur types and their peculiarities in various regions.

³²For details on the distribution of the color forms and races of Caucasian foxes, see Vereshchagin, 1960 (maps).

336 As was often shown above, there is known a directional geographic variation in the phases of color types also (*krestovka*, *sivodushka*, *chernoburaya*).

Fur quality also changes noticeably and regularly. The most fluffy, fine-haired, silky and lustrous furs are possessed by the foxes of the forest zone, especially of Kamchatka and the adjacent districts of East Siberia and the northern Far East. In the steppe and desert zones, the quality of the fox fur is greatly deteriorated—it becomes short and coarse, losing its luster, silkiness and elasticity, the hairs are easily matted. Some of these qualities appear in the open landscapes in the Far North in the tundra zone. On ascending into the mountains, even in southern latitudes, the quality of the pelage is again improved as compared with the plains.

In summary, the reality of geographic variation in the red fox is very nicely characterized by prices in the international fur market: *ognevka* of Kamchatka are 10 times more expensive than gray Turkmenian.

Subspecies of Red Foxes in Our Country

The infraspecific systematics of our foxes is not sufficiently elucidated. This concerns both morphometry and, in particular, color characteristics. Up to the present, only one attempt at a more or less full revision of all forms was made by S.I. Ognev (1931, 1935). This author recognized 20 forms of red fox for the pre-war territory of the USSR. One of these forms he considered a separate species, *V. dolichocrania* but the other 19 as forms of *V. vulpes*, of which two he considered as “tribes” of *V. v. caragan*. Since then, only some remarks were made on separate forms and only very general remarks were made on all forms (Flerov, 1935; Kuznetsov, 1944; Bobrinskii, Kuznetsov and Kuzyakin, 1944), and a review of Caucasian foxes (Vereshchagain, 1960).

The number of forms (20) accepted by Ognev (1931) is too great, but the remarks of Flerov (1935) on the contrary simplify the picture too much. A solid new review of the question is necessary. Preliminarily, if one considers only the best characterized forms (not too “subtle” and generally questionable), 14 to 15 subspecies can, apparently, be accepted for our country.

Below are given only very short characterizations.

1. Middle Russian fox. *V. v. vulpes* Linnaeus, 1758 (syn. *septentrionalis*).

Pelage bright, red, but with strongly developed whitish and yellow ripple on posterior part of back (see above, "Description" section). Fur long and fluffy or of moderate length and fluffiness.

Measurements large. Body length 70–90 cm, weight 5–10 kg.
 337 Maximum male skull length known is 163.2 mm. Some local populations within subspecies limits may on average be somewhat larger (maximum skull length 155.7, condylobasal length 149.6 mm; Kirov district).

In northern and middle (forest) districts of the European part of the country southwards to forest-steppe and eastwards approximately to the Urals.

Outside the USSR—in Scandinavia and probably Central and Western Europe.

The Middle Russian fox is usually accepted, following Ognev (1931), as related to the Middle European *V. v. crucigera* and separated from the north Russian, which is supposed to be the nominal [form]. Foxes of the extreme northern forest zone of the European part of the Soviet Union, as compared to these near Moscow, possess a somewhat longer and fluffier fur. However, in this feature the transition is unnoticeable, the difference not great, and differences in other characters are absent. According to craniological characters, foxes of Arkhangel'sk district, the upper Pechora and Kirov district are completely identical with those near Moscow (V.E. Yakobi). Therefore the separation of two subspecies in this part of the forest zone of the Soviet Union is not justified.

The relationship between the form *crucigera* and the nominal [form] is not evident even for Western Europe. In our materials it

Table 38. Skull measurements of Middle Russian fox (materials from Moscow district; V.E. Yakobi)

Data	Males				Females			
	N.	Min.	Max.	Aver.	N.	Min.	Max.	Aver.
Greatest length	30	138.3	160.5	151.5	26	138.3	158.8	145.9
Condylobasal length	29	135.5	154.8	145.5	26	134.4	147.3	140.3
Length of upper molar row	30	52.2	59.5	55.8	27	50.6	58.4	54.4
Zygomatic width	30	72.8	88.5	79.9	26	73.6	82.7	77.2
Greatest width	30	46.2	51.1	48.6	26	45.1	50.5	48.1

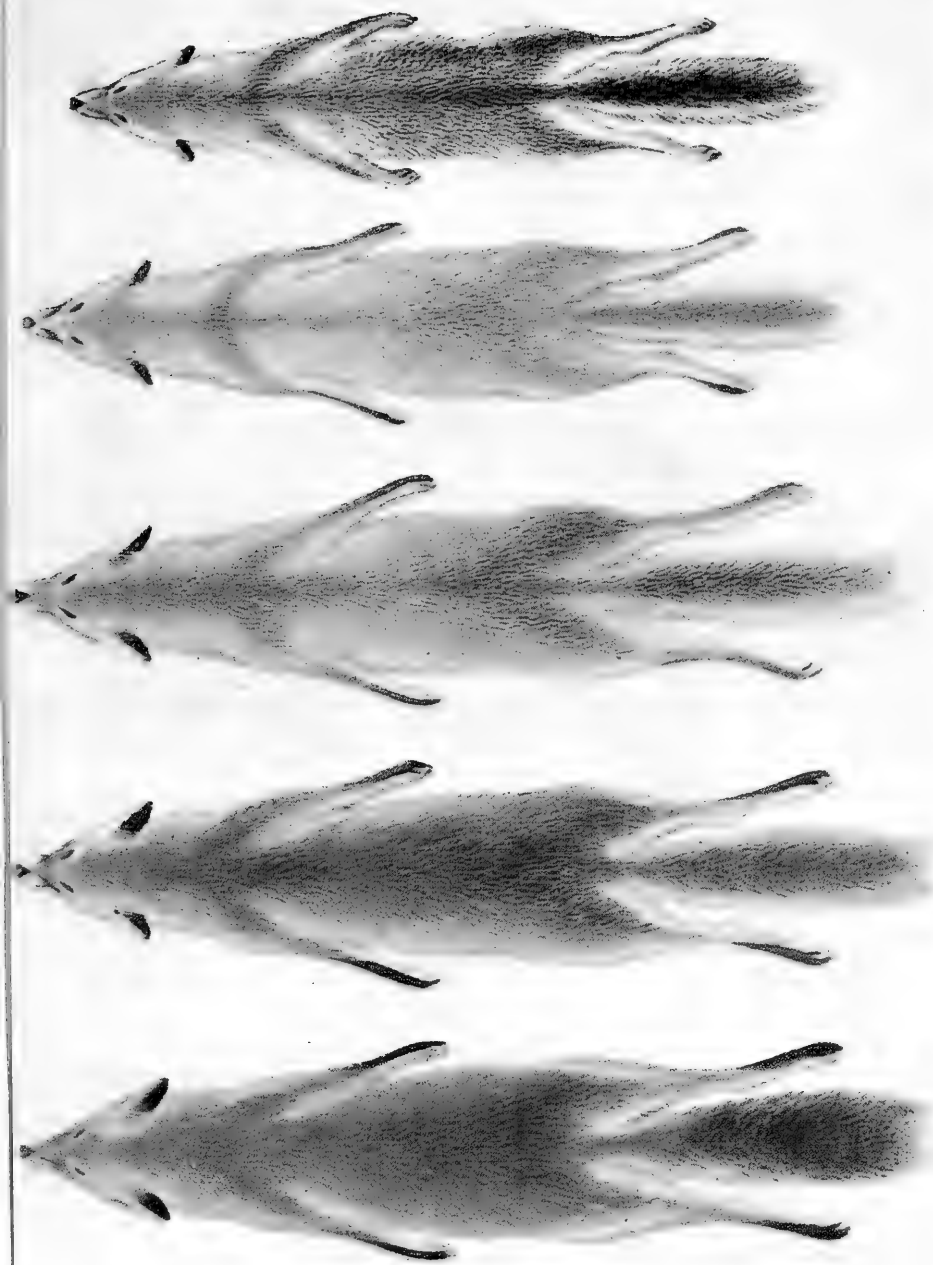


Plate 2. Some types of geographic variation in color of red fox *Vulpes vulpes* L. From left to right: Anadyr fox, *V. v. beringiana* Midd. (Kamchatka, Kronotsk preserve); Middle Russian fox *V. v. vulpes* L. (near Moscow); forest-steppe fox, *V. v. diluta* Ogn. et Vor. (Voronezh district); karaganka, *V. v. caragan* Erxl. (Tabninsk region, Aktyubinsk district); Turkmenian fox, *V. v. flavescens* Gray (near Ashkhabad). Painting by N.N. Kondakov from materials of the Zoological Museum, Moscow University.

is all the more impossible to do. The reality of their differences seems to be doubtful.

At the same time, the close relationship between our northern foxes and the Scandinavian is quite evident and to this there are a series of indications. Therefore, the form described here is provisionally assigned to the nominal one.

2. Forest-steppe fox, *V. v. diluta* Ognev et Vorobiev, 1924.

Color lighter, dull and yellow, not so bright-reddish as in preceding; fur shorter and coarser. Dimensions large—no less than in northern form. Dimensions and proportions of the skull identical to those of Moscow foxes (materials from Voronezh and Poltavsk districts. V.E. Yakobi).

In forest-steppe zone of European part of the USSR.

Not recorded outside the USSR.

This form itself represents a transition from *V. v. vulpes* to the following form.

3. Steppe fox, *V. v. stepensis* Brauner, 1914.

Color somewhat lighter than in *V. v. diluta*, fur shorter and coarser. Measurements insignificantly less than in the preceding form.

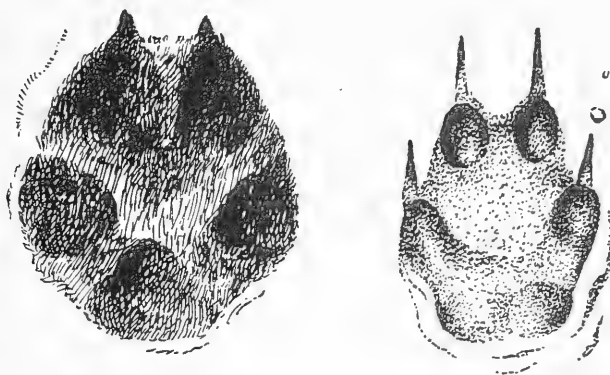


Fig. 122. Difference between tracks of Middle Russian fox *V. v. vulpes* L. and Turkmeniyan *V. v. flavescens* Gray. Left—print of paw of Middle Russian fox on shallow snow; track is broad and diffuse since pads are densely covered with wool, claws quite short and blunt; vic. Moscow, Nov. 1945. Right—track of Turkmeniyan fox on wet sand, paw is smaller, slender, nearly without wool below, claws long and fine; vic. Bakhardok well*, Karakum, 28 Jan. 1948. Sketch by A.N. Formozov, about 2/3 nat. size.

*Misspelled in Russian original, "Bokhudok"—Sci. Ed.

In Pri-Chernomorsk and Pri-Azov steppes; in part in western Cis-Caucasus steppes.

Not recorded outside the USSR; possibly encountered in Pri-Chernomorsk [Black Sea region] steppe regions of Romania and Bulgaria.

- 338 4. Crimean montane fox, *V. v. crymea-montana* Brauner, 1914 (syn. *krymensis*).

Similar in all respects to *V. v. stepensis*, but fur overall somewhat brighter, fluffier and denser.

In mountains of Crimea.

Not recorded outside the USSR.

The separation of this montane, chiefly montane-forest, form cannot be considered well founded. Other characters, mentioned by the describing author and accepted by Ognev (1931), are not well established.

5. North Caucasian fox, *V. v. caucasica* Dinnik, 1914.

Color very variable, from reddish to red-gray and nearly gray, such that in western part of range brighter foxes prevail, but in middle and especially eastern part, grayer ones. Fur short and coarse. Measurements are large, not inferior to those of above-described steppe fox.

In mountains and foothills of northern Caucasus; in part on adjacent plains, except Pri-Caspian part, and probably also south slope of Main range, at least in west.

Not recorded outside the USSR.

Generally, this is well-defined race characterized by very great mixing of characters and general amplitude of variation. On a par with nearly typical gray foxes appearing in the east, bright foxes with relatively good coats are met with in the west, in the Kuban' basin. Most typical, apparently, are "red gray" foxes of the middle part of both the ranges and foothills.

The above-mentioned particularity of this form is, it seems, to a considerable extent connected with the fact that its features are the result of mixing of characteristics of the true montane fox of the Main Caucasus range with characters of foxes of southern Russian and Azov-Black Sea steppes coming in from the west and north, and with characteristics of *karaganka* (in the east) and of montane Trans-Caucasian fox in the south. This form, apparently, itself represents to a certain degree the result of interracial hybridization.

6. Eastern Trans-Caucasian fox, *V. v. alpherakyi* Satunin, 1905.

General color dirty rusty-gray or rusty-brown with brighter rusty stripe along spine. Individual bright-reddish animals are encountered. Fur short, coarse, and sparse. Measurements small. Maximum skull length of males 132–139 mm, females 121–126 mm; condylobasal length in males 130–135 mm, zygomatic width in males 69–76 mm weight to 4 kg.³³

In plains of eastern Trans-Caucasus in Kura and Araks basins on the west, apparently, to Tbilisi; valley of middle course of Araks; Caspian coast north of Apsheron peninsula.

Outside the USSR—in adjacent parts of Iran and, perhaps, Turkey.

This well characterized form belongs, according to characters of size and color, to the group of the southern semidesert and desert foxes—*karaganka*. Together with this, its features, in particular those of the skull, are not manifested to the extent as is found in foxes of Turkmeniya living at the same latitude beyond the Caspian Sea.

7. Trans-Caucasian montane fox, *V. v. kurdistanica* Satunin, 1905 (syn. *alticola*).

Color pale-yellow or light-gray, sometimes brownish-reddish. Fur fluffy and dense—denser and fluffier than in other Caucasian forms. Measurements large—larger than those of *V. v. alpherakyi*, but not smaller, or only slightly less, than north Caucasian form, *V. v. caucasica*.

In Armenian highland and the other montane districts of the Little Caucasus.

Outside the USSR, in parts of Asia Minor and Iran adjacent to Trans-Caucasus.

339 A well-defined form.

8. Anadyr fox, *V. v. beringiana* Middendorf, 1875 (syn. *anadyrensis*, *kamtschadensis*, *kamtschatica*, ? *schrenkii*, *splendidissima*).

Color saturated bright-reddish, almost lacking in bright ripple along back and on body sides. Coat very fluffy and soft.

Measurements large, no less than in foxes of northern European part of the USSR.

³³Available accurate data on dimensions completely inadequate.

In Anadyr territory, Chukotsk land, Kamchatka, Kuril islands and Sakhalin. It is probable that only animals of the northern Kuril islands belong to this form, and Sakhalin foxes are assignable to a separate form (*schrenkii*), while those inhabiting the middle part of the Kuril chain occupy an intermediate position between them (V.G. Voronov and A.G. Voronov). This suggestion requires verification based on good material.

Absent outside the USSR. It is possible that foxes of western Alaska belong to this form (Middendorf, 1875).

The brightest form in the Old World.

9. Yakutsk fox, *V. v. jacutensis* Ognev, 1922 (syn. *sibirica*).

General color of back, neck and shoulders is brownish-rusty, sides bright ochereous reddish-yellow. Coat very fluffy and silky. Measurements large but, apparently, somewhat smaller than in *V. v. beringiana*.

In Yakutia and Siberia southward to Baikal and Stanovoi range and eastward to Okhotsk coast.

Absent outside the USSR.

One of the very brightest forms.

10. Trans-Baikal fox, *V. v. daurica* Ognev, 1931 (syn. *usuriensis*, *dolichocrania*).

Color along spine quite light, dull yellowish-reddish, with strongly developed whitish ripple and grayish longitudinal stripes on anterior side of limbs. Coat fluffy but somewhat coarse.

Measurements large, not less than those of Middle Russian fox.

In Trans-Baikaliya and Amur.

Outside the USSR—in adjacent parts of Mongolian Republic and, probably, northeast China.

Well characterized form, analogous in its geographical position to that of European *V. v. diluta* and very similar to it in color.

Nomenclature of *V. v. daurica* cannot be considered established. If this form is distributed to Peking [Beijing], which is probable, then it follows that it is named *tschiliensis* Matschie, 1907. The name *huli* Sow. given to Manchurian fox is hardly acceptable; it is an evident *lapsus* for *hoole*—the name of an animal from Fukien.

The systematic position of foxes of Ussuri territory (Primor'e) is not clear. It is not excluded that they belong to the described form, although it is more likely that they differ. In that event, they will receive the name *dolichocrania* Ogn., 1926 or *kiyomassai* Kishida, 1929.

11. Tobol'sk fox, *V. v. tobolica* Ognev, 1926.

General color yellowish rust or dirty-reddish with well developed cross, and often black area on belly. Fur is particularly fluffy and long. Dimensions large.

In plains districts of western Siberia in basin of middle and lower course of Ob' river.

Absent outside the USSR.

12. Karaganka, *V. v. caragan* Erxleben, 1777 (syn. *melanotus*).

Color light sandy-yellow or yellowish-gray. Fur short and quite coarse. Measurements are somewhat smaller than those of Middle Russian fox. In skull may be noted same above-described feature as in "gray" foxes.

340 In steppe and semi-desert half of Kazakhstan, including Ustyurt and Pri-Balkhash sands.

Outside the USSR, possibly in western Dzhungariya.

Forest-steppes of southern west Siberia and northern Kazakhstan are, apparently, occupied by a separate form of fox representing a transition from *V. v. tobolica* to *V. v. caragan*. This large fox is quite light reddish-gray in tone; below a dark area is absent. Fur somewhat rough, but quite fluffy. It is, apparently, related to *V. v. diluta*.

In its turn the *karaganka*, features of which are quite variable, itself represents a transition to the next form.

13. Turkmeniyan fox, *V. v. flavescens* Gray, 1843 (syn. *cinerascens*, *splendens*).

Fox of "gray" color, very small size, with small infantile type of skull (see above, Fig. 121 and Table 39). Smallest of all forms

Table 39. Skull measurements of Turkmeniyan fox (vic. Ashkhabad; V.E. Yakobi)

Data	Males				Females			
	N.	Min.	Max.	Aver.	N.	Min.	Max.	Aver.
Greatest length	14	129.3	145.5	134.2	12	128.2	143.9	134.2
Condylbasal length	14	125.7	139.1	132.4	12	122.8	137.4	129.3
Length of upper molar row	14	49.0	54.5	52.7	12	48.6	54.6	52.0
Zygomatic width	14	67.8	76.7	71.9	12	61.5	73.8	69.1
Greatest width	14	44.7	49.6	46.2	12	44.0	47.7	46.2

inhabiting our country—and grayest, with maximum degree of reduction of reddish pigment. Body length 49–57.5 cm, length of tail 33.5–39.5 cm; ear length 7.7–10.0 cm; sole of hind foot 12–15 cm. Weight 2.2–3.2 kg (Southern Tadzhikistan; Chernyshev, 1958).

In plains of Middle Asia approximately south of latitude of Ustyurt and Aral Sea.

Outside the USSR—in contiguous parts of Iran and Afghanistan.

Within limits of USSR, one of most sharply distinguished race of the species. Its relationship to forms described from the more southern districts (see below) may not be considered clear.

Ognev's (1931) suggestion about occurrence of *V. v. splendens*, described from Astrabad in northeastern Iran, in adjacent parts of our country (in southwestern Turkmeniya) was not confirmed. Apparently this form, described from one exceedingly bright specimen, was generally not real. Among the typical "gray" *V. v. flavescens* in southwestern Turkmeniya, fairly bright ginger foxes are sometimes encountered (less than 1%) (V.G. Heptner).

14. Turkestan montane fox, *V. v. ferganensis* Ognev, 1926 (syn. *pamirensis*, *ochroxantha*).

Color quite bright light-reddish or light-yellow, rarely with gray. Fur denser and fluffier (especially in high mountains) than in *V. v. caragan* and especially *V. v. flavescens*. In size somewhat larger than *V. v. flavescens* and similar to *V. v. caragan*.

In mountains of Middle Asia westward to the Amu-Dar'ya.

341 Outside the USSR—apparently in adjoining parts of Afghanistan and China, and in part, apparently, in Tibet. It is most probable, that the actual name of this form is *montana* Pearson, 1836³⁴.

The systematic position of foxes from a series of territories still remains completely unclear. Apparently, foxes of the Yenisei basin, western Siberian forest-steppe and Altai are unique (Kuznetsov, 1944). *V. v. schrenkii* Kishida, described from Sakhalin is, apparently, close to *V. v. beringiana*, or identical to it (fur standards for the Sakhalin fox do not distinguish it). A distinct form, *V. v. splendidissima*, was described for the northern and middle Kuril islands. Information about these forms is completely insufficient (see above, description of Anadyr fox).

³⁴In the following notes, materials of Kuznetsov (1944) were used. In all cases, it was the predominant color type of the species.

For foxes living outside the boundaries of the USSR, a great number of names have been coined. Usually, the forms below are recounted.

In Europe: 1) *V. v. crucigera* Bechst., 1789 (all Europe, except Scandinavia, Spain and some islands of the Mediterranean Sea³⁵; 2) *V. v. ischnusae* Mill., 1907 (Sardinia and Corsica); 3) *V. v. induta* Mill., 1907 (Cyprus); 4) *V. v. silacea* Mill., 1907 (Spain).

In Africa: 5) *V. v. barbara* Shaw, 1800 (Morocco); 6) *V. v. aegyptiaca* Sonn., 1816 (Egypt, Libya); 7) *V. v. atlantica* Wagn., 1841 (Algeria).

In Asia: 8) *V. v. montana* Pears., 1836 (Sikkim, Yunnan; Tibet, Kumaon, Nepal, Punjab to Gilgit); 9) *V. v. pusilla* Blyth, 1854 (Northwestern India from Punjab to Rajputana, Sind, Kutch, Baluchistan, southern Iran, Iraq); 10) *V. v. griffithi* Blyth, 1854 (Afghanistan, Waziristan, northern Punjab); 11) *V. v. japonica* Gray, 1863 (Japan); 12) *V. v. hoole*, Sw., 1870 (southern China from Sichuan to Fujian); 13) *V. v. arabica* Thos., 1902 (Arabian peninsula and Syria); 14) *V. v. tschiliensis* Matschie, 1907 (northern and northeastern (?) China); 15) *V. v. anatolica* Thos., 1920 (Asia Minor); 16) *V. v. palestinae* Thos., 1920 (Palestine and Lebanon); 17) *V. v. peculiosa* Kish., 1924 (Korean peninsula).

In America³⁶; 18) *V. v. alascensis* Merr., 1900 (Alaska and northern part of range eastward nearly to Hudson Bay); 19) *V. v. harrimani* Merr., 1900 (Kodiak Island); 20) *V. v. kenaiensis* Merr., 1900 (Kenai peninsula); 21) *V. v. bangsi* Merr., 1900 (Labrador); 22) *V. v. deletrix* Bangs, 1898 (Newfoundland); 23) *V. v. rubricosa* Bangs, 1897 (region north of Great Lakes eastward to the ocean); 24) *V. v. fulva* Desm., 1820 (eastern and southeastern states east of 100° W. Long. (see footnote 27 on page 482); 25) *V. v. regalis* Merr., 1900 (western parts of Ontario, Manitoba, part of Saskatchewan, and south to Nebraska and Iowa); 26) *V. v. abietorum* Merr., 1900 (British Columbia, northern Alberta); 27) *V. v. macroura* Baird., 1852 (region of the Rocky Mountains south of British Columbia to New Mexico); 28) *V. v. cascadiensis* Merr., 1900 (southwestern British Columbia, Washington, Oregon); 29) *V. v. necator* Merr., 1900 (Nevada, California).

³⁵Two "morphs" of this subspecies were described for Bulgaria—the mountain (*monticola*) and plain (*planicola*) (Atanasov, 1958).

³⁶Many American authors assign their red fox to a separate species, *V. fulva* Desm., 1820.

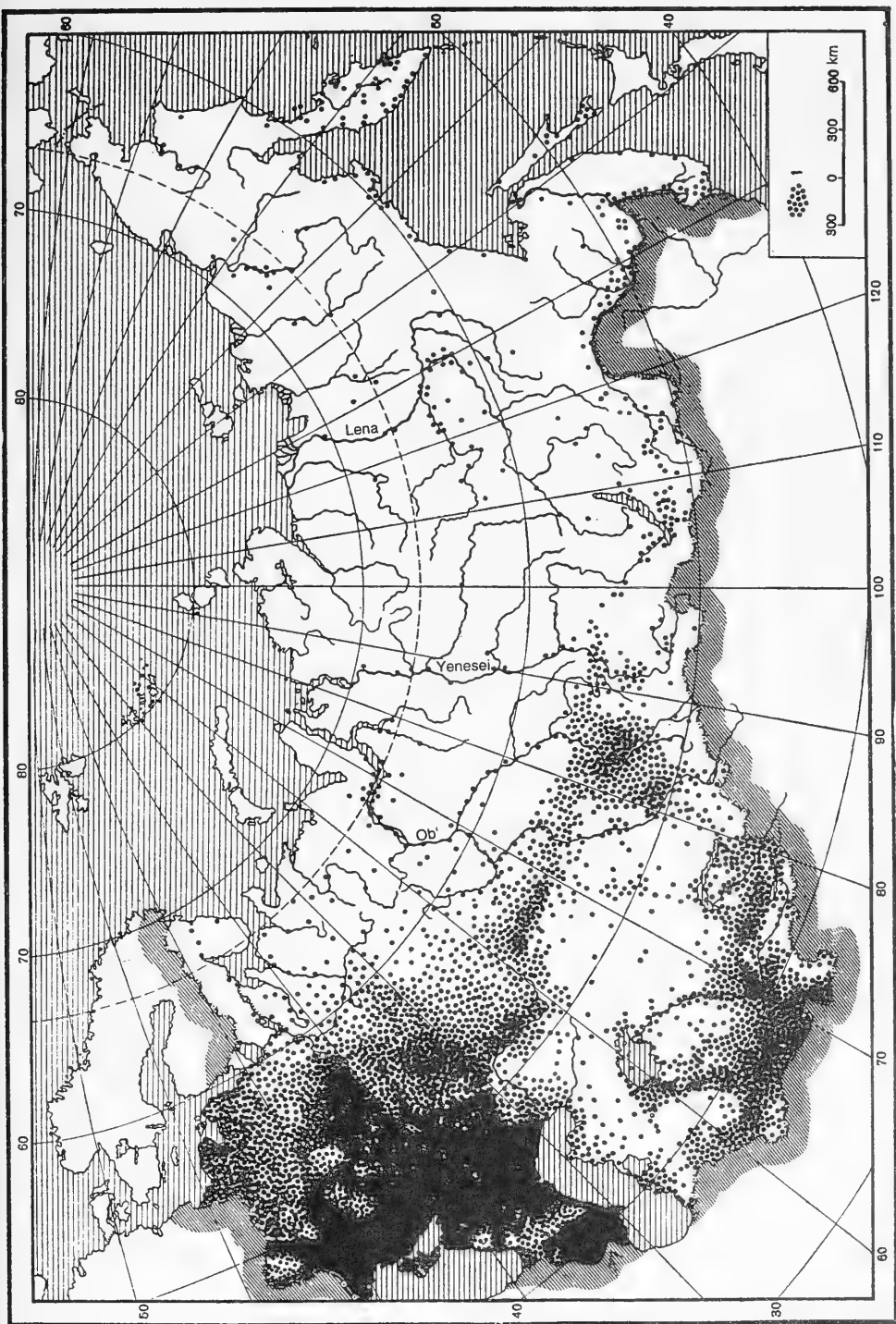
Therefore, about 43–45 subspecies are considered within the limits of the species. This number is, apparently, excessive. Leaving aside forms examined by us, one may a priori note the doubtfulness of the known number of forms of the Old World, and also perhaps the American (though their number is not so great).

343 With all of that, the red fox remains one of the species most remarkable as regards geographic variation (V.H.).

Biology

Population. In the Soviet Union, the fox is one of the most common predators. Proceeding from counts of individuals in restricted areas and annual catch of 80% on the average (Chirkova, 1947 and others), the general population in the territory of the USSR in the post-war years may be determined approximately as several hundred thousand to 1 million head and more (in summer after reproduction in various years).

The number of foxes is not the same in various natural zones and in different biotopes. The species is rare in forest zones with prolonged snow cover and in regions of permafrost—in the north and east of the European part of the Soviet Union, throughout the taiga zone in Siberia and especially in the deep snow districts of western Siberia and Pri-Yeniseisk territory. The fox is rare in tundras—Bol'shezemel'sk tundra, in the southern half of Yamal, Gyadansk and Taimyr peninsulas, and eastward. Some increase in the population density of foxes in the forest and tundra zones is recorded in the southern belt of shrub-tundra and in the forest-tundra. The fox is comparatively numerous in some years in the southern part of Novaya Zemlya, in Kanin, in the lower Kolyma, in the middle and upper course of the Anadyr, in the mountainous country between the Lena and Vitim, in the middle course of the Vilyui, in the taiga of southern Trans-Baikaliya, in Kamchatka, Sakhalin, in Ussurii territory, and on adjacent islands. There are many foxes in the southwestern forest zone in the European part of the USSR. The fox is especially numerous in the steppe zone, in forest-steppe, in the deserts and foothills of the Caucasus, Trans-Caucasus and Middle Asia, where snow cover is absent or does not lie for long, the food is available throughout the year, and the reproductive conditions are favorable (Fig. 123).



342 Fig. 123. Density of fox population on territory of USSR based on yield of skins per unit area. Statistical materials from 1924/25–1954/55 (average per year). Dot refers to 100 skins (A.F. Chirkova).

The density of fox populations in the pre-tundra and forest zones is characterized by the following indicators. In Kanin [peninsula], in the neighborhood of Lake Propashchi, only one fox was recorded when drive-hunting in an area of about 400 km² in a year with minimum numbers (0.03 fox per 100 hectares). On a 10-km route in Pechoro-Ilychsk preserve, for a series of years, only 0.07–0.6* fox tracks were encountered; in the Kharovsk region of Vologodsk district—3.3 tracks on the average, fluctuating in different years from 1.4 to 6.2 tracks (1944–1950); on the Zavidovsk farm in Kalinin district—1.0–7.8 tracks, in Kirov district—0.5–7.0 tracks, but in summer after the appearance of the young 2–3 foxes on 1,000 hectares. In the Pogonno-Losino-ostrovskoe forestry near Moscow, there were 5.8–28.3 tracks on a route of 10 km (average of 20 years), and on 1,000 hectares, an average of 2.1 foxes were counted in winter. In the Smolensk district, in 1,000 hectares, 4 and, in some places up to 10.5 foxes, lived (Table 40) (Teplov, 1949; Chirkova, 1952; B.A. Larin, B.A. Pestov and others).

In the Pri-Yeniseisk taiga, in the middle of the previous century, on a 10 km. route, an average of 0.02 to 0.12 fox tracks were encountered in various years (Middendorf, 1853). In the Magadan district in 1956–1959, on 1,000 hectares of various areas, 0.08–2.0 foxes occurred (Shustov and Belozorov, 1959). On a 10 km route in the Irkutsk district and in the Buryat ASSR, 0.3–3.0 tracks were counted, while in Karagin region of Kamchatka district—0.2–2.3 tracks; in the latter, on 1,000 hectares, 0.2–0.8 and more foxes were met with. In Ul'chsk region of Nizhneamur district, on a 10-km route, 0.2 tracks were encountered and on 1,000 hectares, 1.8 foxes. In the Amur district, on a 10 km route—0.5–3.6 tracks, in Primor'e territory—2.0 tracks, and on 1,000 hectares—1 fox.

One fox burrow was found in an area of 290 hectares near Moscow in a forestry plot of 2,000 to 3,000 hectares in southern Vologodsk district and in the forests of the Far East.

344 In the steppe zone and semideserts in the southeastern European territory of the Soviet Union, the population density of foxes increases 10 times, compared to the taiga region. The fox is especially numerous in the broken steppe landscapes of the Cis-Caucasus, in the Crimea, in the southern Ukraine, in the eastern Carpathians,

*Probably refers to *per* 10 km—Sci. Ed.

Table 40. Index counts of fox populations

Zones, districts	Foxes		Tracks in a 10-km route	Burrows in 1000 hectares
	in 1000 hectares	in a 10-km route		
Forest	0.2–3.0 (to 10.5) ³⁷	0.1–2.0	0.02–7.8 (to 28) ³⁸	0.3–4
Forest-steppe and steppe	0.9–33.0 (and to 48) ³⁹	0–10	2.5–56	1–25 (and to 83) ³⁹
Semidesert and desert	to 24	0–3.5	0–20	2–11
Montane regions of the south	2–20 (and more) ⁴⁰	0.5–2.0	0.5–37.5	12–25

on the right bank of the Don, in the central chernozem belt, in the Orenburg steppe, in the forest-steppe and steppe of the Altai, Minusinsk and Tuvinsk depressions, and also in southern and eastern Trans-Baikaliya, in the steppes of western Siberia and Kazakhstan, and in the semideserts and in part the deserts of Middle Asia.

In the steppes of the European territory of the Soviet Union, fox numbers are greater than in the Asiatic part of the USSR (Izmailov, 1940; Chirkova, 1941, 1947a, 1952a; V. Popov, 1953; Malenkov, 1953; Obtemperanskii, 1955; I. Romanov, 1956; N.N. Bakeev). In a 10-km route, in the steppes of Stavropol'sk territory (at the end of the 30's), an average of 44–56 tracks were encountered, in the Usmansk pine forest of the Voronezh district (in 1948–1953)—from 1.0 to 21.8 tracks. In 1000 ha, in summer, together with the cubs in the litters, foxes amounted to: 0.9 to 3.8 in Brovansk region of Kiev district (1947–1952); in Verkhnekhavsk region at the edge of Voronezh preserve—3–16 (1949–1950); in Staromar'evsk region of Stavropol'sk territory in summer from 3.5 to 12.5 and in winter, 10.3–16.5 (1938–1941). In separate biotopes of the latter region, up to 3–5 foxes were counted in 100* ha, while in the beginning and middle of the 40's, in one place, in winter, around 17–20 and even 30 foxes might be observed, mousing in packs. In the absence of a harvest in the course of a series of years in

³⁷In Smolensk district.

³⁸In Podmoskovsk Forestry plot.

³⁹In small areas in Stavropol'sk territory.

⁴⁰In small parts of former Taldy-Kurgansk district.

*Should be 1000 hectares?—Sci. Ed.

Arzgirsk region of Stavropol'sk territory, on 1000 ha, from 8.8 to 26 foxes were counted in summer of 1938–1941. At the end of the 30's, in Khopersk preserve from 2.5 to 3.5 litters were distributed on 1000 ha in summer, and in winter—10 foxes. In the steppe of Uzhursk region in Krasnoyarsk territory, 2.4 foxes occurred on 1,000 ha.

In desert and semidesert zones, foxes are numerous in many places. They are especially many on the Priergeninsk plain, along the Volga-Ural interfluve, on Ustyurt Plateau, in the Sarysu valley, in southern Pri-Balkhash, and also among the sandy deserts of western and southern Turkmeniya—in Balkhan [mountains] and throughout the entire lowland section southward to the lower Atrek, in Maryisk and Kerkinsk districts, and in the foothills of Kopet-Dag in southern Turkmeniya. Foxes are relatively scarce in Betpak-Dala, in Muyunkum and along the Syr-Dar'ya.

In the Kzyl-Ordinsk district, along a 10-km route an average of 4.1 fox tracks were found (winter of 1940/41); in the northern Kyzylkum and on the coast of the Aral Sea, 0.3 foxes were counted; in southern Ustyurt—0.3 and in the northwest—1.3 animals; in the lower Amu-Dar'ya, only 1 fox was met with in spring, and in
 345 autumn, 1.5 foxes; in former Bel'agachsk region of Semipalatinsk district, in March 1943—3.5 foxes; along the middle and lower course of the Murgab in March, there were more than 10 fresh tracks and a carcass. In the Betpak-Dala desert, in the course of several days not even one fox was encountered. In southern Turkmeniya (Badkhyz), in autumn 1935, 10 foxes might be taken from a ravine near a spring. In Badkhyz preserve, in 1950–1958 (in an annual route of 786 to 4,392 km), in each 100 km of the route, from 1.6 to 7.1 foxes were met with in spring, and in winter from 3.6 to 6.9 head. In Takhta-Bazar region, in 1943, during the day in winter, up to 5 foxes could be seen within shooting distance along an 8-km route. On the Ural-Emba interfluve, in an area of 400 km² an average of 0.3 red and corsac fox litters were encountered per 1000 ha. In Balkhashsk region, in 1,000 ha, there were 0.5 litters; in the vicinity of the city of Gur'ev—2.7 litters (23.2 foxes); in Badkhyz preserve, up to 4 litters (24 foxes) (Kashkarov, 1935; Kolosov, 1935; Rozanov, 1935; Heptner, 1956; Kostin, 1956; Shcherbina, 1961; I.N. Nesterov, A.F. Chirkova).

Foxes are numerous in the mountains and southeastern foothills of the Caucasus and in the Trans-Caucasus, in the Alai mountains

and in the western Pamir, in the Karatau range and along the Pyandzh, in the high-montane belts of Tien Shan (on "syrt"* of the Tien Shan at an altitude of 3500 m above sea level, the fox is common, and in places, even numerous; N. Naumov), in the Dzhungarsk Alatau, in the southeastern Altai, especially in its southwestern foothills.

In the subtropics of the Black Sea coast, foxes are rare, as well as on the southwestern slopes of the Caucasus, in the eastern Pamir and in the forest zone of the Altai and Sayans. Fox is absent in the nival zone and, apparently in the "cold desert" of the Tien Shan.

In the Saraibulagsk, Aiotsdzorsk and Uritsk ranges in Armenia, from 2 to 20 foxes were recorded in the spring and summer in a 1000-ha territory. In the Pambaksk range and in the vicinity of the city of Erevan, in January–March, an average of 3.7–6.0 tracks were met with along a 10 km route; in the vicinity of the city of Kirovakan—36 tracks; in the mountains of the Kirghiz range—37.5 tracks. In the foothill regions of the Altai, in summer of 1946, a year with relatively abundant foxes, 5 litters were found in a territory of 5 km² (Dal', 1944, 1948, 1950, 1954; Chirkova, 1952a; V.N. Belyaev, M.A. Kuz'mina).

Throughout the historical period, fox populations have changed, mainly under the influence of human activity. Thus, in Kamchatka in the 17th century, Krasheninnikov (1755) found such an abundance of foxes that it was sometimes necessary to beat them back with a stick from troughs where the dogs were fed. Many foxes were reported on the Crimean peninsula by Gablitsl' (1785). A.M. Nikol'skii (1889) spoke of the great quantity of foxes on Sakhalin during the past century. [Human] population growth on Kamchatka, Sakhalin and other regions of the Far East and extreme North caused fox harvesting to develop and to a decrease in their numbers. In the deserts of southern Turkmeniya (interfluvium of Tedzhen and Murgab), where the number of foxes is now very high, their number was higher—in the winter of 1886/87, a group of hunters caught 14 thousand foxes and in the preceding year 12 thousand (Heptner, 1956). But, in the greater part of the territory of the Soviet Union, growth of population, expansion of areas under cultivation, thinning of forests in the north, sowing of tall-stemmed

*Elevated watershed.

plants and forest-plantations in the steppe zone, and irrigation and acclimatization of deserts helped to increase fox populations.

Zoologists of the past century frequently noted the low number of foxes in the forest-steppe and steppes of western Siberia. From the mid-'40s of the 20th century, the number of foxes began to increase. Tanning of fox skins in Chelyabinsk, Kurgansk, Omsk, and Novosibirsk districts, and in the Altai territory at the end of the first decade and in the 50's increased several times.

Habitat. Red foxes everywhere prefer open and semi-open expanses. In the tundra and forest-tundra zones, foxes usually are
 346 restricted to the edges of riparian woods, among bushes of floodlands and valleys, along lake shores and rarely *laida* on the seashore. In all seasons of the year, it goes out into the open tundra zone; it is regularly encountered in the subzone of shrub and cotton-grass tundra, preferring elevated relief. In the moss-lichen subzone of the tundra, they appear sporadically. Among the Arctic tundras, the fox is common only in the southern regions of Novaya Zemlya and in the Far East. In connection with climatic warming in the Arctic in the course of the last decade, movement of foxes into the tundra has been noticed (Skrobov, 1958, 1960a). In Magadan district, the fox serves as the main species exploited in the high-bush tundra and is the second species in the zone of Arctic tundra. The distribution of foxes in 1000 ha plots (in a southwestern direction)* in Magadan district is as follows (Shustov and Belozorov, 1959):

Tundras, bushes and swamps of the central subzone of the Arctic tundras	0.08 foxes
Tundras, bushes and swamps of the southern subzone of the Arctic tundras	0.13 foxes
Inundated broad-leaf forests and bushes	1.0 foxes
Inundated mixed forests	2.0 foxes

In the taiga zone, the fox is rare in the depth of the great, remote plain of tall-trunked forests where large areas are occupied by mossy bogs, where soft snow lies for a long time and is very deep. The fox prefers diverse, mixed-age forest among broken relief, and alternating with fields, meadows, grassy swamps and

*Appears to refer to the list of vegetation types, from northeast to southwest—Sci. Ed.

river valleys. It selects biotopes where open areas prevail in autumn and winter. In spring and summer, in the breeding period foxes are concentrated in more remote forest sections. In winter, in Karelia, tracks were encountered along a 10-km route (Marvin, 1959) [as follows]:

in pine forests with berries	—
in pure pine forests	0.43
in pine forests with sphagnum	1.33
in mixed pine and spruce forests	—
in sedge swamps	7.4
in clearings and open burns	7.84
in broad-leaved forests	14.8
average index of occurrence	2.05

In Kharovsk region of Vologodsk district, at the beginning and end of winter, on routes of more than 500 km, 14.7 fox tracks were encountered per 10 km in clearings, 12.4 in sedge swamps, 9.8 in young coniferous forest. From 6.6 to 4.7 tracks were counted in pine forest in a sphagnum swamp, in fields, open swamp, young mixed forest and in meadows; in a young broad-leaved and a mixed grassy forest, 2.8 tracks. The lowest number of foxes visited dense firs—1.2 tracks per 10 km route (B.A. Larin).

In forests in the central zone of the European part of the USSR, foxes hold to various biotopes. From the Byeloruss and Novgorod districts in the west to the Udmurt and Kirov districts in the northeast, the fox is restricted to 72% of cases in autumn—winter time to meadows, fields along edges of forests, beside open swamps among clearings, and floodlands of rivers and creeks. Foxes are encountered in approximately the same biotopes in winter in Sverdlovsk and Chita districts and in the Buryat ASSR.

347 In the forest-steppe and steppe zone, the fox may be met with in all biotopes. It often inhabits places rich in hills and ravines, with access to rocky aspects or with *bairach** forests and also steppes and fields of various kinds, intermixed with islands of forest or thickets of shrubs. On flat steppes in summer, the fox makes wide use, for breeding and shelter from danger, of all unevenness of fields and sown tall-stemmed cereals and technical culture—

**Bairach* refer to forests in deep, flat valleys within the steppes—Sci. Ed.

sunflower, maize, castor bean, wheat, and winter rye, as well as thickets of weeds, ground cherries, isolated groves of birch, aspen, willow, and forest plantations of the broad-leaved variety. After the gathering of the harvest from the fields, the fox hunts even in entirely open biotopes and rests and hides from danger in beds overgrown with weeds, in reed beds, in forest belts, old pine forests, etc.

In the southern zone of grass-forb steppes of Stavropol', average density of foxes in 100 ha (end of the 40's) was in stubble, 5.8 foxes (from 0.3 to 24.0), in fields of sunflowers, castor bean and maize—3.7 foxes in summer and considerably more in autumn; in weeds—3.5 (from 1.3 to 5.6), in speargrass-sagebrush steppes with open gulleys and rocky hillocks with osier—3.3 (from 0.4 to 16.7), in broad-leaved forest, in greenery and in forest gorges on average, 1.2–1.8 (from 0.1 to 60.7; in forest gorges, in some years in autumn, 6–7 foxes were bedded per 10 hectares; N.N. Bakeev).

In the desert and semidesert of the Pri-Caspian, in southern and western Turkmeniya, the fox prefers sandy biotopes with a network of sandy ridges. It is met with particularly often among undulating sand-solonetz of lowlying steppes, grass-sagebrush deserts and steppes, saltsage-sagebrush deserts, and wormwood-turf steppes, in Ustyurt and in the Balkhan [mountains] along precipices and gorges of the low steppe mountains with thickets of various bushes, in saxaul forests and in riparian *tugais* [woodland] along Middle Asian rivers interspersed with open expanses of sands and of *dzhingiliya* [*Halimodendron halodendron*], Russian thistle, tamarisk, pea-shrub [caragana] and other shrubs. Traces of active movement of foxes can be observed among sand dunes and in hills covered in spring with rich grassy cover on the lower course of the Murgab, and also in the impenetrable thickets of reeds and in pistachio groves in the rocky passages in southern Turkmeniya.

In Badkhyz preserve, the fox is also unevenly distributed. For 1950–1956, along a general route of 55,992 km, foxes were encountered per 100 km as follows (Shcherbina, 1961):

in desert-steppe biotopes	1.2
in the Kushka river valley	5.8
in pistachio groves	6.5
average for 2,120 foxes	3.7

Foxes become seasonally redistributed among biotopes. In winter, food attracts many animals and in summer, waterholes on the Kushka river (Heptner, 1956).

The fox is rare in clayey sagebrush plains of semidesert and deserts, and in waterless solonetz depressions of Betpak-Dala. According to counts in the winter of 1940, in Kzyl-Ordinsk district, along a route of 1 km with a light snow fallen 4 days before, 3 tracks were found among the scarce saxauls, in an overgrown clearing in saxaul—1.2, in clearings in saxaul and solonetz steppe—1; in 3 km through old saxaul clearings in hilly desert, and along 50 km in reed thickets, not one track was found (B.M. Kasatkin).

In the Caucasus, the fox inhabits valleys, and mountains to an altitude of 2500–2800 m; it lives in the foothill-steppe, montane forest zones, and montane meadows of the subalpine and alpine zones. It is found in low growing forest, shrubs, and reeds, in weedy areas, fields and open steppes; it prefers rocky and stony places. The fox does not go into the nival zone above 2800 m above sea level. Foxes are rare in the forests of the foothills of the Black Sea coasts and in the tall-trunked beech forests of the southern slope of the Great Caucasus. In Azerbaidzhan, foxes were encountered in virgin semidesert in 59% of cases; in low forests—25%, in beech-hornbeam forests on the southern slopes of the Caucasus—in 6.8%, and in alpine meadows in 3.1% of the cases (Vereshchagin, 1952). In the Pamir-Altai and Tien Shan mountain systems, the fox inhabits all vertical zones, but populations are especially dense in subalpine and alpine meadows to an altitude of 3000–4000 m, approaching the limit of permanent snow. In the Altai and Sayans, the fox is, in the majority of regions, rare, and is restricted mainly to steppe and forest-steppe sections.

In years with food shortages, foxes approach human domiciles.

Food. The fox is an omnivorous predator. In the Soviet Union, up to 300 animal species and several tens of plant species on which it feeds are known. Small rodents constitute the main food of foxes. It feeds most often on various species of gray voles of the genus *Microtus*; in their absence, other species abundant in a given region predominate in the food. Small rodents constitute in the fox diet anywhere from a single individual to 100% of dry weight, and rarely less than several tens of a percent in an analysis. The fox feeds less on birds, of which passeriforms, galliformes and waterfowl

predominate. It often feeds on insects and other invertebrates, as well as on plant food—fruits, berries, seeds and vegetative parts of plants, and along the banks of river and inland waters—on fishes, and along the coast—flotsam (marine animals, fishes, echinoderms and others).

Their food varies in different geographic landscapes (Fig. 124). In the pre-tundra belt and taiga zone, the northern voles *Microtus middendorffi*, *M. oeconomus* and *M. agrestis* serve as the chief food, and rarely, species of the genus *Clethrionomys*. Mouse-like rodents were encountered in food analysis as follows: up to 93% in Lapland preserve, to 70% on Kola peninsula, 62% in the Middle Kolyma region and Kamchatka, 90% (of 100% occurrence) in eastern Sayan ("Stolby" preserve), 35–38%, during an abundance of small rodents in the Middle Sakhalin preserve (Nasimovich, 1948; Dul'keit and Kozlov, 1958; L.P. Borodin, A.I. Zubov, A.V. Kondratov, A.N. Shcherbakov, E.P. Volkova). In the extreme North the fox, in the absence of gray voles, destroys a great quantity of lemmings of the genus *Lemmus* (up to 67% in winter in Lapland preserve).

With a scarcity of small rodents, it catches forest game birds (up to 40% occurrence in Lapland, 24.6%—in Pechoro-Ilych, 12–14% in Middle Sakhalin, and 5.3% in Sayan ("Stolby") preserves); willow ptarmigan, capercaillie, hazel grouse and black grouse. In same years, it often catches white hares (up to 15% occurrence in Lapland and up to 52.7%—in the Pechoro-Ilych preserves). The forest game birds and white hares are consumed in great quantities only in years of epizootics and pestilence among them. Especially many white hares were devoured by foxes in Yakutiya in years of massive epizootics and die-off of this rodent* after its legendary reproduction in 1955–1957. At that time more than half of the foxes examined had fed on hares (more than 50% occurrence in analyzed food and 96% occurrence in feces of 2 fox litters; Labutin, 1960). In other years, foxes consume hares comparatively rarely (in Middle Kolyma region 3.9% occurrence in food, in Middle Sakhalin preserve in summer, 8% and in winter 6%; in Kamchatka and in "Stolby" preserve, in analysis of some tens of stomachs and feces of foxes, hares were not encountered, and only in preserve territory were found in 2 cases out of 8 remains of fox feeding).

In the Far East, the massive migrations of salmonids—chum, humpback, silver and others, which are stranded on river banks at

*Sic—Sci. Ed.

the time of spawning are of significant importance for foxes. Composition of the food of foxes on the Kuril islands is unique; on Urup Island, in August 1955, the main feeding areas were along the seashore. In feces and stomach contents there was no predominant food; it consisted mainly of flotsam and the only rodent there—the gray [Norway] rat—and also insects (in 24 fecal and stomach content samples, % occurrence was as follows; Shmeleva, 1958):

gray rat	75
birds	88
fishes	65
insects	100
crustaceans	72
sea urchins	37
plants	83

Of constant occurrence in the food of northern foxes are sedges, grasses, needles of spruce and fir, hazel [*Corylus*] and Japanese stone pine [*Pinus pumila*] fruits. Foxes consume great quantities of berries of crowberry, red bilberry, huckleberry, blueberry, raspberry, mountain ash, rose, hawthorn and others.

In the southern belt of the forest zone of the European territory of the Soviet Union, mouse-like rodents, in years when they are scarce, are not always used as the main food. Besides all of the animals possibly inhabiting the forest, foxes feed on carrion (up to 50% by weight and up to 100% occurrence in food analyses in regions near Moscow in some years), usually around human dwellings, in poultry yards, on garbage, eating edibles, and even unedible wastes—scraps of leather, rags etc.

In the forest-steppe and steppe zone, the fox feeds almost exclusively on small rodents, the chief of which consist of ground-dwelling individuals which remain active throughout the entire year. In the Ukraine, mouse-like rodents are encountered in 91.3% of fox foods investigated; of nine species, that which was eaten more often than others, within a 7-year period, was the common vole (*Microtus arvalis*)—75% in winter and 62% during the whole year (Korneev, 1956; see below, Table 42). In the Stavropol' steppe, during a 4-year period, only 2 vole species were met with as food—common and social (*M. socialis*) voles—in 95–100% of cases in various years (see below, Table 41). In the southeastern European

territory and in the steppes of western Siberia and Kazakhstan, the particular species that serve as food are the narrow-skulled vole (*Microtus gregalis*) and the sagebrush vole (*Lagurus lagurus*); in Tselinn territory (former Akmolinsk district) both species in June 1946 constituted 90% of occurrences in the food (A.F. Chirkova). In the forest-steppe of Novosibirsk and Omsk districts, mouse-like rodents, during a period of sharp change in their number, constituted from 17 to 84% of occurrences in the food of some tens of foxes by season (L.A. Popova, A.F. Chirkova).

In warm times of year, the fox hunts various species of the gray ground squirrel [*Spermophilus* sp.]. Their remains were encountered in the food of the fox as follows: in the Ukraine, 2.3% (Korneev, 1956), in the forest-steppe of Voronezh district—up to 38%, in the black soil forb-grass steppe of Stavropol' territory—13%, in the northern forb-grass steppe of Saratov district—47% and in the semidesert virgin sheeps-fescue-needle-grass steppe of Arzgirsk region in Stavropol'—67% (A.F. Chirkova). In forest-steppe regions of Novosibirsk and Omsk districts, the fox excavates ground squirrels even in winter (8% of occurrences in stomachs; L.A. Popova).

Snakes and lizards were found in the food of foxes in 30% of occurrences in the Cis-Caucasian steppes. Insects (mainly beetles and grasshoppers)—in Stavropol' territory in a series of years—30%, and in separate seasons of the year in Stavropol' up to 62%, in Kiev district—60%, in Saratov district—30%, and in Tselinn territory (former Akmolinsk district)—50%. Of the plant foods, the fox eats fruits of several fruit-trees and cultured melons, and in years of
 352 rodent scarcity, it avidly eats rose hips which are rich in vitamins as well as the wheat grains and sunflower seeds (V. Popov, 1943; A.F. Chirkova).

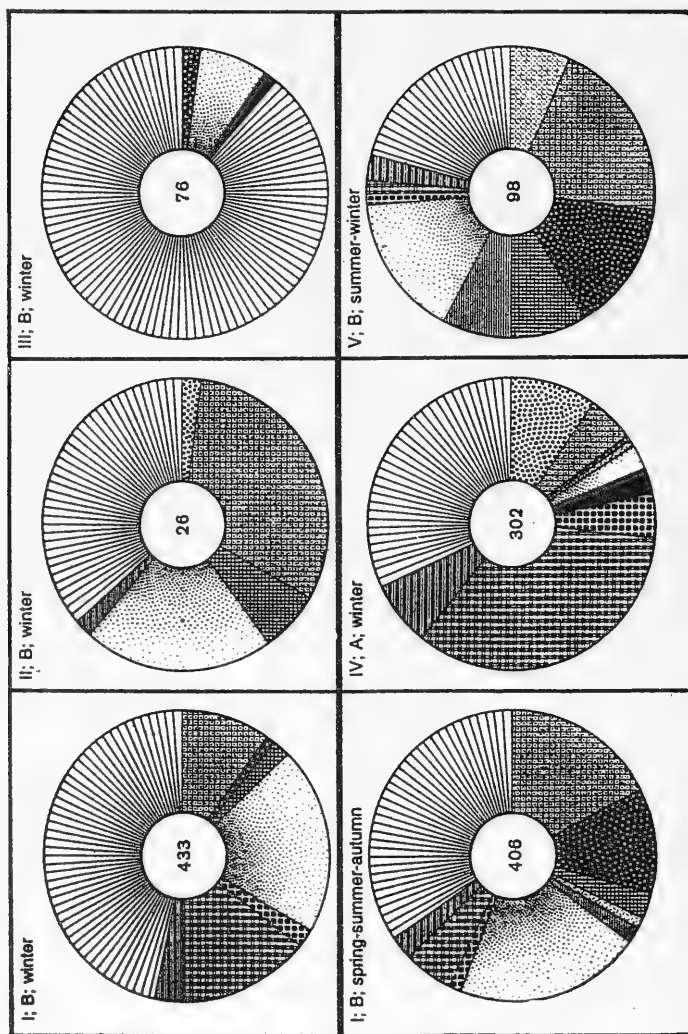
The various species of gerbils constitute the main food of desert foxes, depending upon their natural abundance. In the Volga-Ural sands, foxes fed mainly on midday gerbil (*Pallasiomys* [= *Meriones*] *meridianus*) and tamarisk gerbil (*Meriones tamariscinus*). In the Kyzylkum and Karakum, foxes usually hunt the great gerbil (*Rhombomys opimus*); however, in spring 1946, in the sands of the lower and middle course of the Murgab river, they fed more on midday gerbil (61% of occurrences in feces) and more rarely on great gerbil (25%). Dry weight of remains of gerbils in food constituted 84% (A.F. Chirkova). In the lower course of the Ili river

in spring and summer of 1939–1941, half of the foxes examined fed on four gerbil species, most often on great gerbil—5–40% in various years, more rarely on tamarisk gerbil—up to 17%, then midday—up to 10%, and red-tailed—up to 15% (I.G. Nitsenko, V.N. Belyaev, A.A. Sludskii). In southern Turkmeniya, in years of Afghan vole (*M. afghanus*) reproduction, the fox feeds mainly on it (up to 80% of occurrences in food in the territory of Badkhyz preserve in foothills of Kopet-Dag; Shcherbina, 1958). Among jerboas, foxes more often hunt the thick-tailed three-toed (*Scirtopoda telum*) and the large species of the genus *Allactaga*. Tolai hare [*Lepus tolai*], which is usually difficult to find in the southern Pri-Balkhash, is often hunted by foxes in years of its epizootics (48% of occurrences in feces in June 1939; A.A. Sludskii).

In the years when small rodents are scarce, the main substitute food (though not as fully valuable) is served by insects⁴¹. In northern semideserts, they constitute in some years up to 70% of occurrences in food analyses. In the deserts of Kzyl-Ordinsk district, the fox feeds, in addition, on solifugids, scorpions and tarantulas (up to 45% of occurrences in food around Lake Telikul'); in southern Turkmeniya, foxes feed heavily on termites, beetles, grasshoppers and others—up to 97% of occurrences of all invertebrates in food of foxes in pistachios (1956) and up to 98% in the Kushka river valley (1954); aggregate for 5-year period—in 70.8% of cases. In Uzbekistan, insects were met with in food on an average of 70.9% over 5 years. The red fox fairly frequently feeds on lizards, turtles, snakes and their eggs, destroying many vipers in years of their mass appearance. Plant feeding is also of great importance, constituting in pistachios of Turkmeniya an average of 12.8%, and in some years up to 48% of occurrences in analyses. Chief among these is the pistachio nut—up to 74.8% of occurrences, and also capers, watermelon, various grasses and seeds. In Uzbekistan, the plant food constituted over 5 years an average of 74.5% of occurrences in the food, of which the main ones are: grape (20.2%), grass, wild olive and others (Shcherbina, 1958, 1962; Ishunin, 1961, 1963; Formozov and Osmolovskaya, 1963). In the Tersko-Kumsk sands, in October 1957, fox ate an abundance of ephedra fruits (*Ephedra* sp.; Bakeev, 1959).

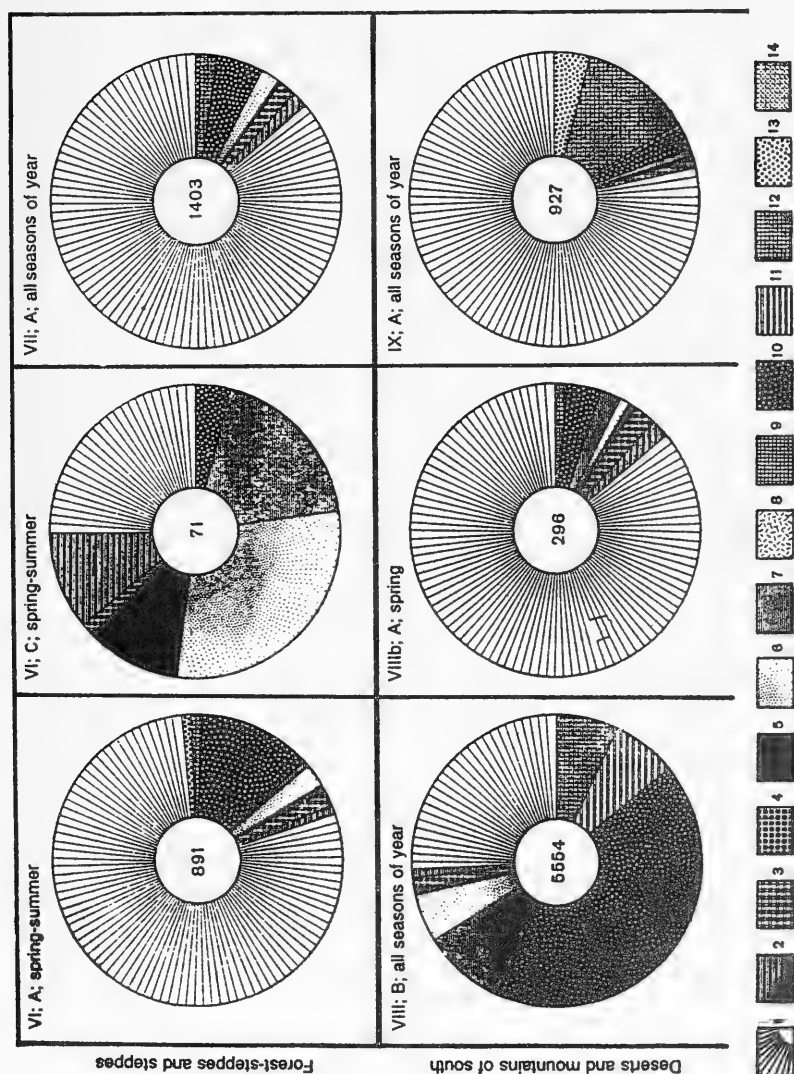
⁴¹With such food, reproduction of foxes falls (Chirkova, 1948).

Fig. 124. Components of food of foxes in various natural zones and seasons of year (contents of stomachs, intestines, feces, food remains near the burrows, etc.). I—Lightly wooded forest and montane tundra of Kola Peninsula (Lapland preserve; Nasimovich, 1948; II—Deciduous forest-tundra and montane tundra of former Srednekolymysk territory (A.I. Zubov); III—Montane taiga of eastern Sayan ("Stolby" preserve near Krasnoyarsk; Kozlov and Dul'keit, 1958); IV—Middle taiga and southern taiga and mixed forests of the plains of central and northern districts of the European part of USSR (A.F. Chirkova); V—Coniferous forests (taiga) and Pacific Ocean shore of Sakhalin (Middle Sakhalin preserve; E.P. Volkova); VI—Forest-steppe of Kiev district (A.F. Chirkova); VII—Chernozem [black soil] forb-grass and semidesert sheep-fescue-needle-grass steppe of Cis-Caucasus



(Stavropol' territory; A.F. Chirkova); VIII—Deserts of southern Turkmeniya: a—Badkhyz preserve (Shcherbina, 1962); b—lower Murgab [river] (A.F. Chirkova); IX—High mountain Trans-Caucasus (Dilizhansk valley; Armenia; A.F. Chirkova). A—in % of dry weight of the remains; B—in % of occurrences; C—in % of inedible remains near burrows:

1—rodents, mainly voles; in desert—gerbils; 2—hares; 3—carrion; 4—small carnivores; 5—insectivorous mammals; 6—birds; 7—reptiles; 8—amphibians; 9—fishes; 10—insects; 11—other invertebrates; 12—plants; 13—unidentified and inedible remains; 14—marine animals. Figure in centre of each diagram refers to the number of objects examined.



In the mountains of the Crimea and Caucasus, the fox also feeds most often on small rodents. In the mountains of Armenia near Kirovakan, they constituted from 50 to 98% of the dry weight of remains in feces and from 65 to 100% of occurrences in various months from 1936–1939. They ate gray voles of the genus *Microtus* more than others, mainly *M. arvalis*, but also quite often *M. socialis* which, together with woodland voles (genus *Pitymys*) and the locally rare snow vole (genus *Chionomys*), constituted 85% of specimens (of 1727) of all mammals in these investigations. Cases of feeding on brown hares were rare (less than 0.1% of dry weight of remains and 1–1.5% of occurrences). In all seasons of the year, although not many times, fox hunted insects (up to 42% of occurrences), mainly locust, beetles, and grasshoppers (A.F. Chirkova). In the Crimean mountains, the fox attacks young and weakened individuals of adult roe deer (up to 29% of occurrences in food; Kotovshchikova, 1936). In orchards, they select windfalls of apples, pears, cherry plum, bird-cherry, blackthorn, grape and others; they eat musk- and other cultivated melons.

Catching small rodents becomes very difficult with snow cover, especially in the second half of winter with much snow, and also after a thaw, when an ice crust forms in the course of a winter of intermittent snow cover. The fox usually cannot break these crusts, and because of this catching of rodents is delayed. In such years, foxes turn to any living food available to them, and in their absence, to carrion, refuse from human households, and even to feces of animals and humans. Everywhere, in years of starvation, the fox consumes small insectivorous mammals—shrews, water shrews [*Neomys*] and moles—which are most frequently only caught and discarded, and usually not utilized by it as food, and sometimes (even more rarely) feeds on small carnivores—weasels, ermine, even marten and others, which usually constitute about 1% of occurrences among its food remains. However, in the mid 30's, when numbers of small rodents were low in central forest districts of the European territory of the Soviet Union, small carnivores were eaten by fox often, and, for instance, were found in the stomachs of four foxes (of 12 caught). In these years, the stomachs of foxes were at times completely full of hedgehog remains, swallowed along with the skin as well as quills of these animals, which protruded into all sides, bulging out from beneath the thin wall of the stomach (A.F. Chirkova).

Age differences in foods of foxes are insignificant. In the Stavropol' steppes, and in the deserts of southern Pri-Balkhash, food of young is more variable than adults.

In foreign countries foods are also varied. In Bulgaria, small mouse-like rodents serve as principal foods, and more rarely, hares (11% of occurrences in diet, part of which consisted of cripples), then carrion, less—various birds; in summer—insects and other food, quite often—fruits, berries, cultivated melons (Atanasov, 1958). In Finland, the fox feeds mainly on domestic garbage and small mammals (hares 6%, other species—less; Lampio, 1952). In England, they often feed on rabbits, rarely on hares, and also on refuse and carrion; in the absence of rabbits, mouse-like rodents and carrion appear as the main foods (Lever, Armour and Thompson, 1957). In the eastern and middle states of the U.S.A., the food of the red fox consists of rodents, insects, birds, carrion and several other animal groups. The main food is mouse-like rodents of the genera *Microtus* and *Peromyscus*. In separate regions, muskrat, pheasants, grasshoppers and fruits are significant. In forests of the state of Michigan (Murie, 1936), the fox often eats hares* of the genus *Sylvilagus* and voles of the genera *Synaptomys* and *Microtus*, as well as beetles, etc. (Nelson, 1933, Hamilton, 1935, 1943, 1944; Errington, 1935, 1937; Findley, 1956 and others).

The food composition of fox greatly varies in one and the same place by year and season, and also by biotope, depending upon the abundance and availability of one or another food. In the chernozem [black soil] herb-grass steppe of the Staromar'evsk region of Stavropol' territory, the feeding regime of the fox changed annually and seasonally according to the number of mouse-like rodents (Table 41). A decrease in remains of secondary food species in feces and stomachs serves as a characteristic index of food favorability of the fox in this region. They were filled with mouse-like rodents in the years 1937/38 and 1940/41; on the contrary, remains of various secondary foods in seasons of decrease in numbers of small rodents, and the small amount of the latter in feces and stomachs in autumn and winter 1938/39, 1939/40 and in the summer of 1940 indicated unfavorable nutritional conditions.

In the Kushka valley (southern Turkmeniya, 1954), the fox diet varied extraordinarily with the seasons of the year. In spring and

**Sic*; the proper group name is cottontail rabbit—Sci. Ed.

354 **Table 41. Contents of feces, stomachs and intestines of red foxes in chernozem herb-grass steppe of the Cis-Caucasus in various years (in % of occurrence in analysis; A.F. Chirkova and N.N. Bakeev)**

Food type	Year and season, number of objects	Winter, 1937/38, spring 1938	Winter, 1938/39, spring 1939	Autumn and winter, 1939/40	Spring, beginning of summer 1940	Autumn and winter 1940/41
		70 feces	310 feces, 4 stomachs and intestines	32 feces, 30 stomachs and intestines	491 feces, 2 stomachs and intestines	12 stomachs and intestines
Mouse-like rodents		100.0	100.0	95.2	100.0	100.0
Ground squirrels		—	13.0	—	8.8	—
Brown hares		12	6.5	9.5	5.9	—
Insectivores		—	6.5	—	3.0	—
Carrion, animal wastes		—	8.5	16.7	5.9	16.7
Birds		6.3	24.0	16.7	61.8	25.0
Reptiles		24	13.0	—	14.7	—
Insects		24	52.2	11.9	61.8	—
Plants		6.3	24.0	64.3	17.6	75.0
Inedible wastes (rags and others)		—	—	2.4	3.0	—
Unidentified		—	—	2.4	—	8.4

summer, insects served as the main foods (97.7% of occurrences), mainly termites, locust and beetles; small rodents were encountered in 1.1% of occurrences. In autumn and winter, insects constituted only 58.1%, but mouse-like rodents increased significantly (18.6%), especially the Afghan vole, reptiles and carrion; hedgehogs disappeared, and the number of the species of passerine birds significantly decreased (Shcherbina, 1958).

Variations in the fox diet in the Ukraine by season of the year are considerably less (Table 42). During 7 years of investigations in various areas, foxes consumed 118 animal and 25 plant species. The greatest variety of food was discerned in summer and autumn (83 and 80 species), and less in spring and winter (40 and 56 species). Mouse-like rodents remained the main food group through all seasons of the year, constituting 97.5% of occurrences (among the remains of all mammals), of which voles were 76.5% (Korneev, 1956).

355 Table 42. Main food types in diet of red fox in the Ukraine by season of the year (in % to numbers of different data; after Korneev, 1956)

<div><div></div><div>Food type</div></div> <div>Period, quantity of data</div>	Spring	Summer	Autumn	Winter	Yearly
	177	170	181	198	726
<i>Mammals</i>					
Red-toothed shrews [<i>Soricinae</i>]	3.3	1.7	4.4	2.0	2.9
Brown hare [<i>Lepus europaeus</i>]	7.9	14.1	3.8	11.1	9.2
House mouse [<i>Mus musculus</i>]	—	4.7	6.6	12.6	6.1
Harvest mouse [<i>Micromys minutus</i>]	—	2.3	5.3	5.0	3.3
Striped field mouse [<i>Apodemus agrarius</i>]	14.6	2.3	9.4	5.1	8.1
Common field mouse [<i>A. silvaticus</i>]	7.9	12.9	9.4	10.0	10.0
Sagebrush vole [<i>Lagurus lagurus</i>]	—	—	4.9	5.1	2.9
Northern red-backed vole [<i>Clethrionomys rutilus</i>]	2.2	4.1	5.3	3.0	3.7
Water vole [<i>Arvicola terrestris</i>]	36.7	21.1	17.6	7.5	20.3
Field vole [<i>Microtus agrestis</i>]	20.9	11.7	10.5	7.0	12.0
Common vole [<i>M. arvalis</i>]	61.5	50.6	60.2	75.7	61.7
<i>Birds</i>					
Passerines, not further identified	3.3	3.5	5.3	0.5	3.2
Domestic fowl	0.6	7.0	1.1	2.5	2.7
<i>Reptiles</i>					
Sand lizard	1.7	5.8	3.3	2.0	3.2
<i>Insects</i>					
Mole-cricket [<i>Medvedka</i>]	6.2	14.1	6.0	0.5	6.4
Ground beetle	1.7	8.8	1.1	—	2.7
Dung beetle	0.6	7.6	1.6	1.5	2.7
May cockchafer beetle [<i>Melolontha</i>] larvae	—	5.3	3.8	—	2.2
<i>Plants</i>					
Sugar beet	—	—	2.7	5.5	2.2
Pear fruits	0.6	2.3	11.6	0.5	3.7
Carrion; farm animals and dogs	6.7	1.2	4.4	7.0	4.9

In the Darvinsk [Darwin] preserve in the shore zone of the Rybinsk reservoir, the fox ate more mouse-like rodents in April–June (80% of occurrences in diet), when they were left unprotected during times of flooding, than in August–October (72% of occurrences); in the central part of the preserve, rodents were more often eaten in autumn (93.7%) as compared to spring (76.9% of occurrences). Consumption of secondary foods varied by biotopes, especially hares, ducks, amphibians, fishes and mollusks. The ratio of food types varied sharply depending upon the volume of spring flooding. In winters following heavy spring floods, when mouse-like rodents almost disappeared, they had little significance in the fox diet, and after a spring with little water, they constituted, on the contrary, the main food of the fox. In the first case, the significance of secondary foods was strengthened—hares, insectivores, all species of birds, fishes, plants, carrion, human domestic refuse (Kaletskaya, 1957).

Variations in the diet of the fox in different biotopes of southern Turkmeniya is very indicative (Table 43). In the Kushka valley and in the pistachios, insects served as the main food and in the Kushka valley, almost exclusively insects and arachnids. In desert-steppe biotopes, small rodents stood in first place in the diet, but in years of low numbers (1958), the fox also fed on insects and lizards, skinks and tortoises.

Home range. The fox home range usually occupies an area of several square kilometers. In the central forest belt of the European part of the USSR, its diameter is equal to 6–10 km. The size and character of the biotopes of the home range change depending upon the season of the year, and food abundance. As a rule, during the breeding period, especially in years of food abundance, the home range diminishes, but in the autumn–winter period and with food scarcity, it enlarges considerably; in years of starvation the fox moves into biotopes not usual for it near human settlements. After dispersal of the litter, foxes hunt and feed singly. In the case of disease or injury, the fox always strives to reach its home range. The individual home ranges of foxes, especially in winter time, overlap each other. In the steppes of the Cis-Caucasus in some years, it was possible to observe tens of foxes mousing simultaneously within one field of vision.

In Lapland preserve, in winter, the fox develops a territory of 30 to 50 km² and more. Judging by marking [of foxes] in the forests of Kalinin district, one fox litter one and a half years old in winter held

356 Table 43. Diet of foxes in various biotopes in southern Turkmeniya (Badkhyz; spring-summer 1954 and 1958; findings in % of number of samples investigated⁴²; Shcherbina, 1962)

Years, biotopes Food type	1954			1958	
	Pistachios	Kushka river valley	Desert- steppe	Pistachios	Desert- steppe
Mammals	30.9	2.6	75.0	21.2	60.7
Insectivores ⁴³	0.5	0.6	0.7	—	—
Hares	0.1	—	—	1.2	0.1
Mouse-like rodents	28.2	1.1	73.0	20.0	60.6
Birds	8.1	3.4	19.0	2.3	9.1
Bird eggs	0.2	—	—	—	—
Reptiles	8.0	0.8	2.4	24.7	35.8
Tortoise eggs	0.6	0.3	—	1.2	6.1
Arachnids	21.8	10.0	2.4	14.1	4.5
Insects	86.1	97.7	26.9	91.8	56.6
Myriapods	0.2	—	—	—	—
Pistachio nuts	1.9	—	—	24.7	—
Other plants	—	5.4	—	—	—
Carriion	2.1	0.9	1.3	—	—

to a total distance of 2–3 km from the burrow. In the forest-steppes, foxes roam considerably more widely. On the left bank of the Dnepr (Kiev district), the young foxes of one litter were caught in the course of a summer in various burrows at distances no greater than 4–5 km from their birth place, but in winter, not only this litter but also others usually dispersed in a radius of 15–40 km and in individual cases emigrated more than hundred kilometers from the burrow; young
356 foxes went out several tens of kilometers in the Tatar ASSR (Nasimovich, 1948; Chirkova, 1955; A. Popov, 1956).

In the course of 24-hr period, from one bedding-down to the next*, foxes in the Lapland preserve and in Stavropol' territory moved up to ten kilometers, and in severe freezes—more than 30 km (Sabaneev, 1904). On another day, the line of their tracks sometimes continues farther, sometimes returns backwards, repeating the previous route.

⁴²In 1954—2780, in 1958—1275 samples (mainly feces).

⁴³82% hedgehogs.

*In the Russian original, *ot lezhki do lezhki*; lit. "from lying down to lying down"—Sci. Ed.

Foxes feeding on carrion, or on carcasses of animals killed by wolves, sharply contract their hunting territories. They remain at the carcass for days and sometimes weeks, and after feeding, several individuals lie up in the nearest bog. In Lapland preserve, their home range is no more than 5–8 km²; when resting, the foxes lie several hundred meters from food source*, rarely up to 1½–2 km. In forest reserves near Moscow, in the winter of 1951/52, distinguished by a small quantity of small rodents, from 3 to 5 foxes fed on discarded scraps of meat from a nearby slaughterhouse, and on a route of 6–7 km there in April, 20 tracks of foxes encountered roaming in the vicinity of the food source; in January, before the trimming of the meat, a 15-km route intersected a total of 4 tracks evenly on this route. In the Brovarsk region of Kiev district, from 2 to 8–10 foxes approached baits placed in six areas near dens of summer litters (Nasimovich, 1948; A.F. Chirkova).

In coniferous forests of Manitoba in Canada, individual fox territories have a diameter up to 19 km, but in summer are two times smaller (Seton, 1909). In mixed and deciduous forests of the USA, hunting territories cover tens and hundreds of kilometers (Arnold and Schofield, 1955), but in the center of Europe, marked fox cubs ranged a distance of several hundreds of meters to ten kilometers, rarely farther (Niethammer, 1937; see below, “Seasonal migrations and transgressions”).

Burrows and shelters. The choice of places for burrows is guided by protection, soil and feeding factors. Red foxes prefer to construct their burrows far from populated places, but cases are known of
 357 burrows in immediate proximity to human habitation. Burrows are often situated on the slopes of hills and mountains or in ravines, bluffs and steep banks of rivers, lakes and seas, in irregular lands—ditches, depressions, gutters, in clefts of rocky defiles, and also neglected gullies, in places that are neglected, abandon, and usually not flooded by high waters. Sometimes, they are restricted to parts of forest, shrubs, or thickets of weedy grass and shrubs, to fields of tall-stemmed cultivation—cereals, sunflowers and others, to thickets of reeds, canes and sedges. In the forest, foxes often dig burrows among the roots of tall-trunked trees.

In the north, the fox constructs its burrows most often on slopes, usually in forested sections giving way to tundra, more rarely in shrub tundra, and very rarely in the moss or lichen tundra, where it some-

*In Russian original, *privad*; lit. lure, bait—Sci. Ed.

times occupies burrows of Arctic foxes. It digs burrows in light, dry, sandy, sandy loam, clay-loam; well-drained soils. In the central forest zone of the European part of the USSR, the burrows of foxes reach the subsoil layer or the lower part of the alluvial layer (Kolosov, 1935a). When excavated among the roots of trees, they can serve for many decades, and if partly destroyed, they are rebuilt anew; in the steppes, burrows are used for several years (A.F. Chirkova).

In deserts, fox burrows are situated on sand dunes and in saksaul stands, in the Badkhyz preserve, often in colonies of the great gerbil [*Rhombomys opimus*]. Here, the fox also uses burrows of porcupine [*Hystrix leucura*], wolf and other large animals. Of 118 burrows here, 65.3% were in great gerbil colonies, 22.9% were independently dug, 7.6% in porcupine burrows and 4.2% in the clefts of rocks and erosion channels (Shcherbina, 1961a, 1962). In sandy deserts, burrows are easily destroyed.

In particular areas where there are rich food reserves with good conditions of protection—among rocky outcrops of limestone having natural solution chambers, or near broad stands of reeds in the open

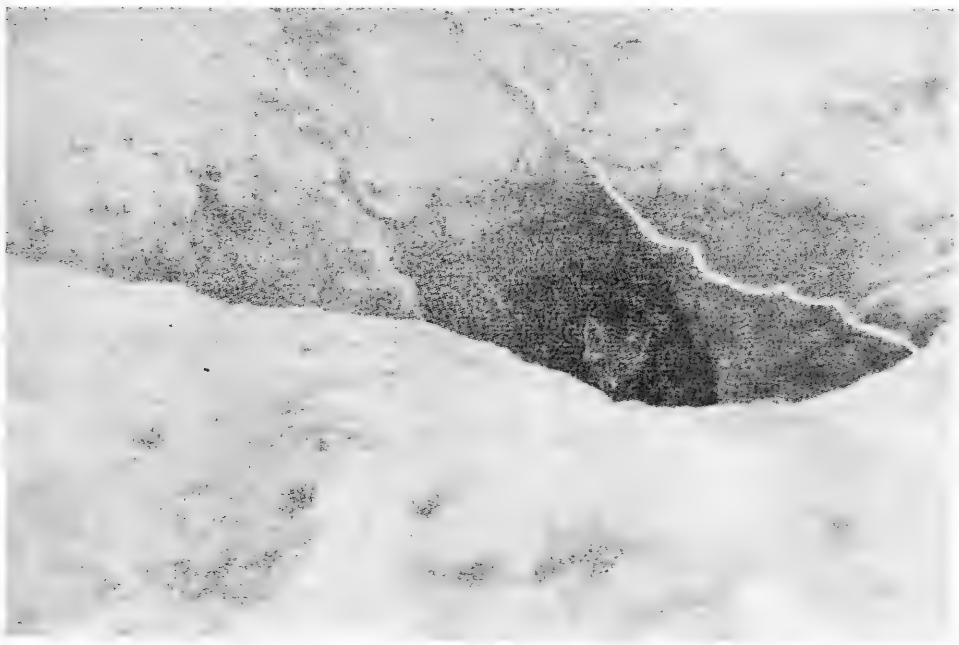


Fig. 125. Den burrow of red fox in arable land. Voronezh district. Photograph by A.F. Chirkova.

358 steppe, foxes live in colonies, constructing many tens of burrows in a small expanse (Cis-Caucasus, Chirkova, 1947, 1952a; Crimea, N.D. Emel'yanova). In the Staromar'evsk region of Stavropol' territory, an extent of 4 km of rocky outcrops within the hilly steppe, 40 burrows were constructed, which were used for the cubs in various years. In the Manych [river] steppes along heavy growths of reeds on the flood plain of the Chograi river, up to 80 burrows were dug along an 8-km segment of which 11 were occupied by litters during one season (Fig. 130).

In the forest-tundra, burrows are situated on southern, southwestern and southeastern slopes of hills; in the steppe zone, western slopes are preferred, and in deserts—northern slopes. The main entrances to the burrows are also oriented to the plane of the surface. Temporary burrows in the deserts of southern Turkmeniya are often dug with the opening to the south, probably in relation to the northerly winds that prevail here in summer.

In contrast to the burrows of Arctic foxes, badgers, marmots, and corsac fox, which are sometimes occupied by foxes, the burrows that



Fig. 126. Entrance to a burrow of a single male; its feces in front of the burrow. Voronezh preserve. Photograph by A.F. Chirkova.

they excavate are usually not characterized by great complexity (Fig. 131). They are divided into den and temporary burrows; the latter consist only of one short passage or small cave dug for concealment. Den burrow construction is somewhat more complicated: the main entrance leads downwards (at 40–45°), broadening to form a den, from which passageway side-tunnels branch in various directions the locations of which vary greatly. In the forest-steppe of Kiev district, along the passage of a burrow, there are from 1 to 3 widenings layered with grass or leaves. In Kolyma, the nesting chamber was 35 cm high and 50 cm in diameter. In the Ukrainian steppes and in the desert of northern Pri-Aral and southern Turkmeniya, burrows have up to 3–5 entrances, but those located in colonies of gerbils—up to 15; in Ust'yurt, there are often 2 entrances, and in the forest around Vychegda, up to 3 entrances. In the steppes of the Manych [river], individual den burrows of foxes possessed up to 32 entrances; apparently, the red foxes occupied the burrow of a corsac fox (Kostin, 1956; Shilova, 1960; Shcherbina, 1961; A.I. Zubov, A.F. Chirkova).

359 In the Far North, from 2 to 10 entrances are known (Iokhel'son, 1898; Sokol'nikov, 1927; Portenko, 1941); apparently, the burrows with a large number of entrances belonged to Arctic foxes.

Depth of the burrows ranges from 0.5 to 2.5 m; usually they do not extend to ground water. Length of the main passage on a straight line reaches 17 m, standing at 5 to 7 m on the average (Kiev district, Stavropol', Badkhyz preserve). Diameter of the inner passages of the burrow in steppe soil is 15 to 20 cm in height and 25 to 30 cm in width; in desert soils the dimensions of the burrow are larger; width of the main entrance is 30 × 40 cm and more, usually rounded or oval in section, sometimes of nearly slit-like form, its height—up to 70 cm.

In spring, during the cleaning of the burrow, the fox, with strong, rapid movements, at first with front paws, and then with a kicking movement of the hind feet, throws the discarded soil a distance of 2–2.5 m. After the appearance of the young in the burrow, this soil is trampled, forming a spot on which the fox cubs play and to which the parents bring food. The general area of the den burrow is from 12 to 72 m², on average—40 m² (Kiev district); in the deserts of southern Turkmeniya burrows with areas from 7.4 to 52.8 m² are known (Shcherbina, 1961a; A.F. Chirkova). Rarely, red foxes litter outside a burrow, in a hollow or near the fallen trunk of a tree, in a pile of firewood logs in the forest, etc.



Fig. 127. Entrance to the den burrow of a Turkmeniyan red fox, built in a great gerbil [*Rhombomys opimus*] colony. Badkhyz preserve, southern Turkmeniya. Photograph by E.I. Shcherbina.

360 When the young animals begin to grow up, foxes usually change burrows due to parasitic infestation (Kiev district, Badkhyz preserve).

Daily activity and behavior. Red fox activity depends mainly upon feeding conditions. In places where the fox is fairly free from pursuit, it may be seen mousing at any time of day or night. Preferred hours of hunting are early morning before sunrise and late evening—beginning of night. The fox spends a longer or shorter time in hunting

depending upon the abundance of food. Often, it rests in the hot midday hours and, apparently, for a short period in the dark time of night. When the foxes go in search of food, the fox cubs come out of the burrow and play, but hide themselves at the slightest danger; when the mother returns, the cubs suckle and feed on the food provided, after which they play for a while and go into the burrow for a rest. In the evening, this picture is repeated.

At the end of summer, after the litter leaves the burrow, the animals experience a wandering life in search of food, at first together with the mother, lying down to rest in one or another burrow. In autumn, after the final dispersal of the litter, and later—in winter—the young foxes scatter and feed singly. By the time of first snowfall, the young foxes are inactive for two–three days and lie up anywhere in a protected place. In autumn and winter, the adult foxes and the growing young spend almost all the time in the open air, resting in forms between feeding hours. The young foxes often retreat into burrows, usually in wet weather or hiding from danger. Both adult and young foxes in the middle regions [of the country] in the very severe frost (-30°C and below) usually spend the day in burrows (V.G. Heptner).

The red fox feeds on carrion only in the late hours of the evening and in night, and leaves at sunrise. If the carrion is visited by wolves, the fox follows after them early in the morning.

In the second half of winter, with the onset of estrus, one can see “wedded” foxes in midday. In the park on Pogonno-Losinoe Island in
 361 Moscow, and in Byelorussia, four males happened to be observed running after one female (Serzhanin, 1955; A.F. Chirkova), and in the steppes of Voronezh district (Ognev and Borob'ev, 1924)—up to 10 males, who yelp and fight among themselves. At the time of rut, foxes are very excited and almost never rest.

After mating, the female cleans the burrow and leads a more secretive way of life; at the end of pregnancy she spends most of the time in the burrow. In the first days after birth of the cubs the mother does not leave the burrow, and the male brings her food. After that, the male mostly avoids the litter and lives alone, occupying one or another empty burrow; some males do not accept sharing in the feeding of the fox cubs.

The daily cycle of foxes varied geographically, depending chiefly on differences in main foods (nocturnal, diurnal, crepuscular animals) and the climatic factors (temperature, wind force, precipitation), as

well as upon human activity. Thus, in some places in the deserts, where it is not especially persecuted, it fears man very little. In the beginning of the 40's in the Badkhyz preserve "the behavior of foxes takes sometimes the form of such 'trustfulness' as is never observed, for example, in the European part of the Soviet Union. In June, one fox visited the site of the expedition for several successive days, either in the evening or at dawn, and coming within a distance of 100–150 meters, barking sometimes for half an hour without a pause; it was not even disturbed by activity which prevailed in the camp during formation of the caravan composed of eleven pack animals. At night, foxes traveled along their paths passing within 10–15 m of sleeping people. In the 30's, in the Kushka valley they stole the provisions from tractor-drivers in camp. Sometimes in the daytime foxes approached to within 100–150 m of wells and left only when frightened" (Heptner, 1956).



360 Fig. 128. A litter of Turkmeniyan desert foxes, *Vulpes vulpes flavescens* Gray, by a burrow in the open desert. A badran trunk, *Ferrula badrakema*, is nearby. Badkhyz preserve, southern Turkmeniya. Photograph by Yu.K. Gorelov.

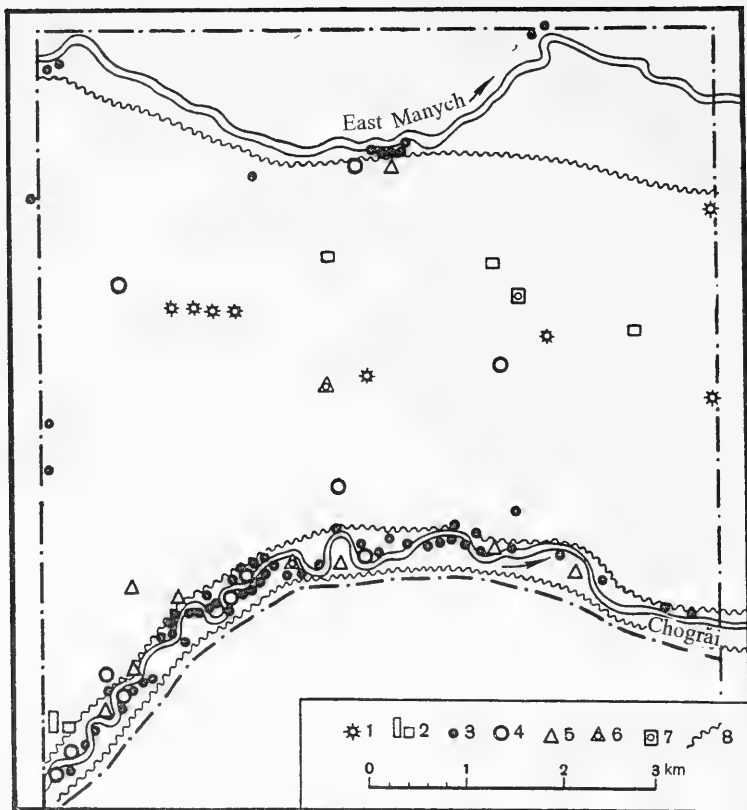
At the northern border of the forest—in the Lapland preserve (Nasimovich, 1948), the red fox in summer is more active at night while in the winter time—in the morning. Here, foxes go hunting 1–2 times per day/night, and hunt with short pauses. In the taiga of the Fast East, foxes are very cautious and feed in the evening or early morning (Slyunin, 1900).

In the steppes of the Cis-Caucasus, foxes always hunt in daytime, but, only in the period of reproduction; the adults do this more



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Fig. 129. Old den burrow of the Turkmeniyan fox in pistachio grove in the mountains of Gyaz'-Gyadyk. Badkhyz preserve, southern Turkmeniya. Photograph by E.I. Shcherbina.



362 Fig. 130. Section with a high concentration of fox burrows in floodplain of Chograi river, overgrown with reed. Virgin steppe along the East Manych [river], Stavropol' Territory (from Chirkova, 1947): 1—Hills; 2—Farms, sheep-folds; 3—Fox burrows without litters; 4—Burrows with litters, 1938; 5—Burrows with litters, 1939; 6—Burrows in which there were litters both years; 7—Burrow of corsac fox with litter, 1939; 8—Flood plain border.

stealthily, and at the end of summer and in autumn, inexperienced young foxes are often encountered approaching humans at close range. In the desert in summer, the fox often never goes abroad at all in daytime, protecting itself in the burrow from sunstroke. At the same time, even in the very hottest time of year, for example in the Badkhyz desert, foxes sometimes continue to hunt until 8–9 o'clock in the morning and later, when it is already hot and the sun shines strongly, and in the evening, it hunts long before the sun sets, when the heat

has only started to decrease. This is, apparently, connected with the fact that one of the chief food items of the fox—the great gerbil—is a diurnal animal. Besides the mentioned period, and especially in winter, foxes in Turkmeniya are, to a considerable degree, active during daytime. This is partially explained in that several rodents serving them as prey, for instance red-tailed gerbil [*Meriones erythroua*], are active in summer mainly at night, but in the period when it is not hot, turn to a diurnal mode of life (V.G. Heptner). In general, foxes in nature are distinguished by broad individual variability in behavior and daily rhythm.

Seasonal migrations and transgressions. More or less regular seasonal movements of foxes are known for the northern margins of the [Soviet] Union, the deserts, and the high montane regions. In the extreme North, after a mass appearance of small rodents, there is an

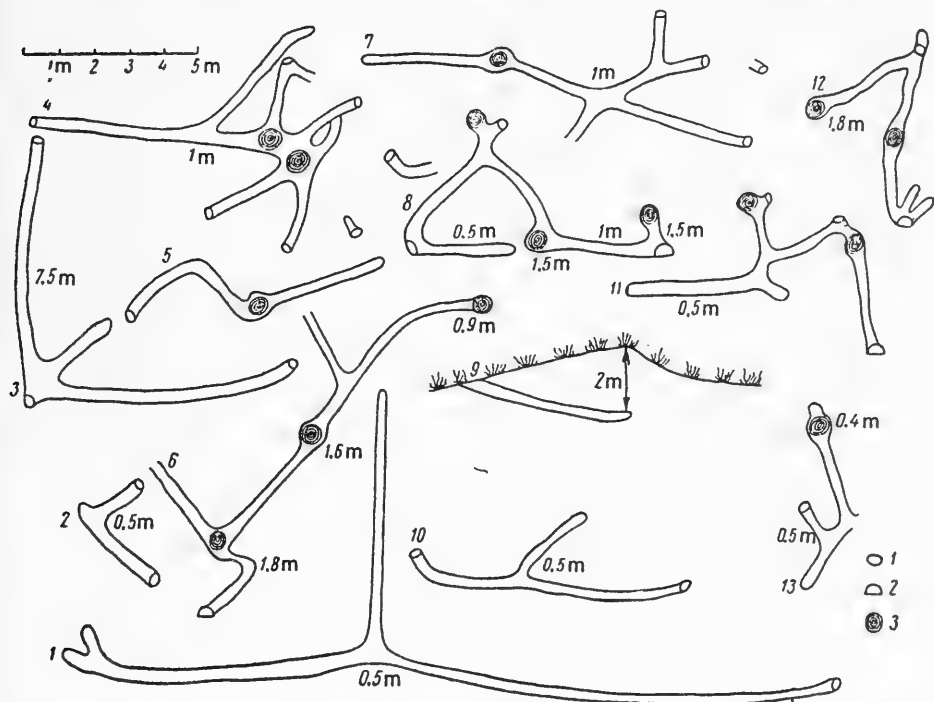


Fig. 131. Scheme of construction of fox burrows (A.F. Chirkova). Steppes of the Cis-Caucasus: 1—in sandy meadow; 2—in water meadow (with litter). Forest-steppe of Kiev district: 3, 5, 6, 8, 11, 12, 13—among arable land or winter rye (with litters), 4, 7, 9, 10—in forest or shrubs (with litters, except 10). 4, 6, 8—former badger burrows. Figures near nest or at separate parts designate depth under surface: 1—exit openings, 2—main exit, 3—nest (see legend).

increase in number of foxes, which immigrate to the tundra searching for food. The farthest known transgression of foxes outside the breeding zone is to Novaya Zemlya, the coast of Kara Sea northeast of the Bol'shezemel'sk tundra, the northern extreme of Yamal, northern Gydanskiy Peninsula, Dixon Island, the central part of the Taimyr Peninsula to 72.5°N. Lat., Lyakhovsk Island below 73–74°N. Lat. and Wrangel' Island, 300–700 km from places of reproduction of the species (Middendorf, 1869; Zhitkov, 1913; Mineev, 1935; Heptner, 1936; M. Popov, 1953; N.V. Provorov). In addition to meridional [N–S] migrations, latitudinal [E–W] migrations also exist—for example, as in the Arctic fox, from the lower Pechora to Malozemel'sk tundra and from Timansk tundra to Kanin Peninsula (Semenov, 1936; A.F. Chirkova). In Kholmogorsk region of Arkhangel'sk district, a red fox
 364 was killed which had been marked 600 km to the northeast in Malozemel'sk tundra (Parovshchikov, 1956).

In the course of the last decades, colonization by foxes has been taking place in the forest-tundra and southern tundra. Its frequent transgressions and, sometimes, breeding is observed in the entire European tundra belt, with the exception of the extreme northeast. Advance to the north was also observed in Yakutiya and in Magadan district (Skrobov, 1958, 1960, 1960a; Shustov and Belozorov, 1959).

With deep snowfall in the forest zone, migration of foxes into the floodlands of large rivers occurs, and in Kamchatka and Sakhalin—to the seashores.

In the forest-steppe of Kiev district and the Tatar ASSR, by marking on paths, it was shown that over 1–2 years, the majority of foxes dispersed a distance of 15–30 km, some of them, 2–5 km and only one in Kiev district was caught 120 km from the place of release. Emigration of foxes in the course of a year for several tens of kilometers is also confirmed by recording of transgressions of individuals ill with mange (Chirkova, 1955, 1957; A. Popov, 1956).

In southern Turkmeniya—Badkhyz preserve—foxes in winter spread more or less uniformly over the territory; at this time, waterholes do not play any role in the animal's lives. In summer time, inhabitation deep in the desert becomes difficult for it due to the distances to be traveled to water. In this connection, in the hot time of year, foxes, if they do not abandon these regions of the desert completely, then in all events their habitation here is notably reduced. Movements take place in two directions. The population of Badkhyz foxes, on the one hand, gathers on the periphery—in the valleys of Kushka,

Egri-Gek and Tedzhen rivers, where some small pools of water remain, and on the other, they more or less concentrate near the wells. Water remaining in wells from the watering of sheep is used at night by foxes (Heptner, 1956).

In the mountains of the Caucasus and Trans-Caucasus, Middle Asia and the Altai, in September–October, with the falling of deep snow, foxes descend from the alpine and subalpine zones to the forest belt and lower. In the Sayans they wander down to less forested places where the snow is not so deep. The movement of foxes from the high mountains to the lower forest belt takes place also in Kamchatka. The reverse movement of foxes to the mountains in spring is less obvious.

Reproduction. The red fox reproduces once per year, in spring. Some females become capable of reproduction at the age of 9–10 months and give birth to young at the age of one year.

All females become sexually mature at the end of the second year of life.

In the middle latitudes, the preparation for estrus in females begins about two months before it starts, in the majority of cases in December. The organs of reproduction proliferate in a definite sequence, changing internally and increasing in dimensions. At first, the neck of the uterus swells. The vagina thickens by almost three times, its inner epithelial layer becomes cornified, which is characteristic for the beginning of estrus; in the mucous secretions of the female, clumps of exfoliated epithelium are observed. Obvious growth of the uterine horns begins about two weeks before estrus; at the time of estrus, the uterine horn increases almost double, becoming resilient and elastic. At the time of estrus, the ovaries increase 1.5–2 times; follicles in it mature, forming Graffian vesicles. Ovulation in the fox is spontaneous; i.e. not dependent on copulation. The mature follicles rupture not simultaneously and in their places *corpora lutea* appear, in connection with which fertilization is possible at various times by [different] copulatory acts. At the moment of estrus, the sexual organs of females attain the greatest degree of swelling and elasticity.

In nature, the sexual cycle in males begins in August–September, when the process of sperm formation begins, causing swelling of the testes. The testes attain their greatest weight in December–February when the spermatozooids mature; at that time, sperm appears in great quantity in the seminiferous tubules and in the epididymus (Chirkova, 1941, 1947, 1954, 1960) (Fig. 132). In the silvery-black fox in

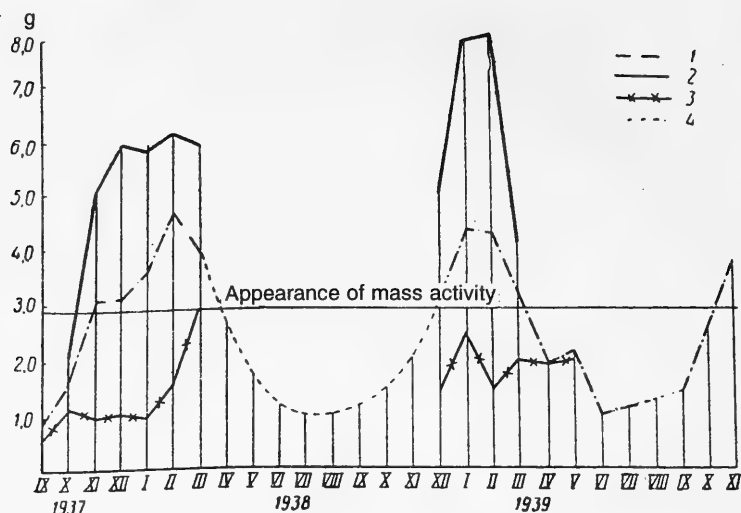


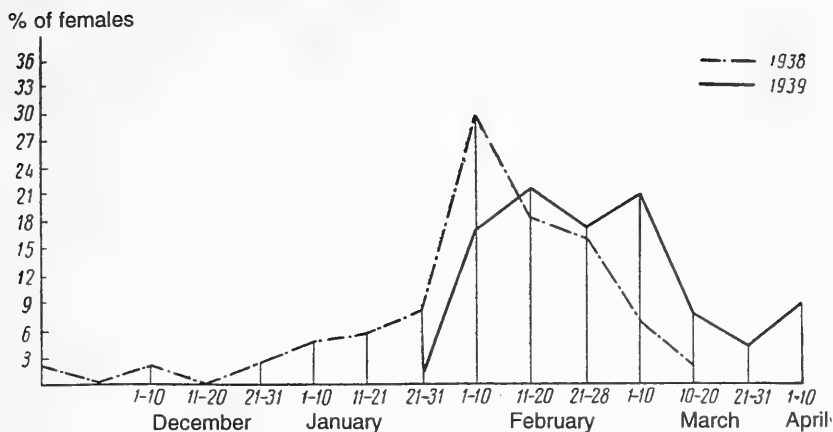
Fig. 132. Sexual cycle of the male red fox (by testes weight) in successive years with various feeding conditions (from Chirkova, 1947): 1—average weight; 2—maximum weight; 3—minimal weight; 4—presumed path of curve (no materials).

captivity, the appearance of prostate gland secretion, essential for insemination, is delayed by 1.5–2 weeks as compared to the testes.

The female permits the male to copulate for a period of several days; in this time, the mammary glands of the female swell to 0.5 cm in diameter (Zaleker, 1937, 1939; Starkov, 1937; Il'ina, 1952; Kler, 1953). In fur farming, cases of repeated copulation are known, which occur when fertilization does not take place the first time, after abortion or death of the new-born cubs. Copulation is accompanied by a copulatory tie between male and female which sometimes continues
366 for more than an hour. After mating, the fertilized eggs are implanted in the horns of the uterus on the 8th–10th day. Pregnancy in foxes lasts from 49 to 58 days, often 52 days.

Foxes often copulate in burrows (Cherkasov, 1867 and others). Up to 13⁴⁴ fox cubs may occur, on the average, 4–6. The lactation period lasts 1½ months. The young foxes remain in the burrow about 1.5–2 months. Playing and searching for food, they gradually begin to go farther from the burrow, and finally do not return to it any more, leaving together with the mother. Already in August, in middle latitudes, young foxes begin to lead a fully independent life; in

⁴⁴Up to 14, according to unverified data.



365 Fig. 133. The course of estrus in the red fox of European part of the USSR for two successive years (1938–1939) with different feeding conditions. Percent of females in estrus to the total number of examined females. Materials from 10 steppe, forest-steppe and taiga districts (from Chirkova, 1947).

southern steppes, this takes place in July and in the years of poor food conditions—in June.

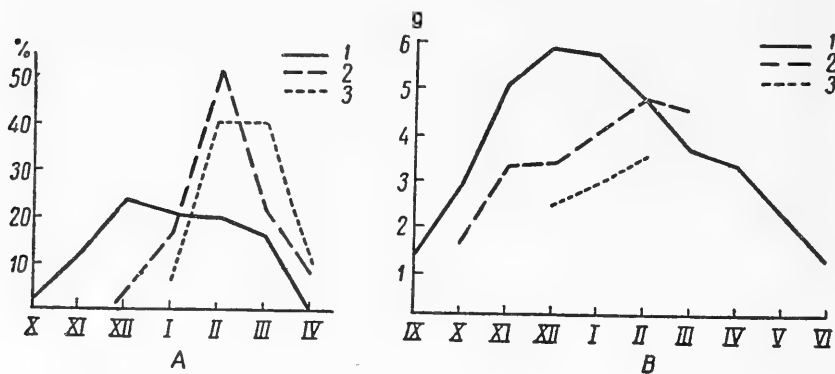
Reproduction of the red fox varies both geographically and by year (Figs. 133, 134); the time of reproduction and fertility both vary (Chirkova, 1960, 1961). Reproduction in the desert and steppe zones occurs earliest of all, while in the taiga and forest-tundra zones, it is significantly later. In the southern steppes, estrus in the female red fox occurs most often in December–February, in the forest zone of the European part of the USSR, in February–March, and in the forest-tundra zone, they come in heat in March–April. The testes of males attain their maximal weight in the southern steppes in December, in the northern forest-steppe—in February, and in the forest zone—February–March. Within the whole forest zone of the USSR, rut of foxes continues for 5 months. Separate cases of rut in all zones end usually in April.

Fox cubs appear at the burrows mainly $2\frac{1}{2}$ to 3 months after the beginning of estrus in females. In the forest zone of the European part of the USSR, whelping occurs chiefly in April, and fox cubs appear near the burrows in the course of May–June. In the steppe zone, the fox gives birth to young primarily in March–April, and the young animals appear near the burrows in April–May. Litters are found at

the burrows in the entire territory of the steppe and forest-steppe zones, and probably, in the forest zone, during about 5 months.

In the deserts and semideserts, red fox reproduction is greatly prolonged. In Badkhyz preserve (southern Turkmeniya) the first signs of the onset of nuptial times are observed in November, when the foxes begin to move in pairs. Especially intensive mating is observed in December and comes to an end January. Whelping takes place in February–March. The first early litters were observed in the middle of February (Shcherbina, 1958). Here, fox cubs are met with at the burrows during the course of 7 months. In montane regions, judging
367 by separate observations reproduction takes place in the various belts at different times; in the lower, it starts nearly simultaneously with the surrounding plains, while in the higher it is delayed.

The appearance near the burrows of the first litters of fox cubs in the deserts is sometimes noted already in January, in the steppes and some montane regions of the south, from January–February, in the forest zone from March–April, and in the northern forest zone and in the forest-tundra, from May and later. All times of reproduction are, on the average, delayed in a northeasterly direction both for the territory of the Union as a whole, and in each natural zone. In the territory of the entire Soviet Union, the time of appearance of litters of fox cubs on the surface extends for half a year (Fig. 135).



366 Fig. 134. Variation in the sexual cycle of the red fox in various natural zones of the European part of the [Soviet] Union (from materials of a series of years, from Chirkova, 1960). A—Estrus in females according to the laboratory determinations in % of the total number of examined specimens; B—Weight of male testes: 1—southern steppes; 2—northern forest-steppe, mixed forests and southern taiga; 3—northern taiga. Months are plotted on the abscissa.

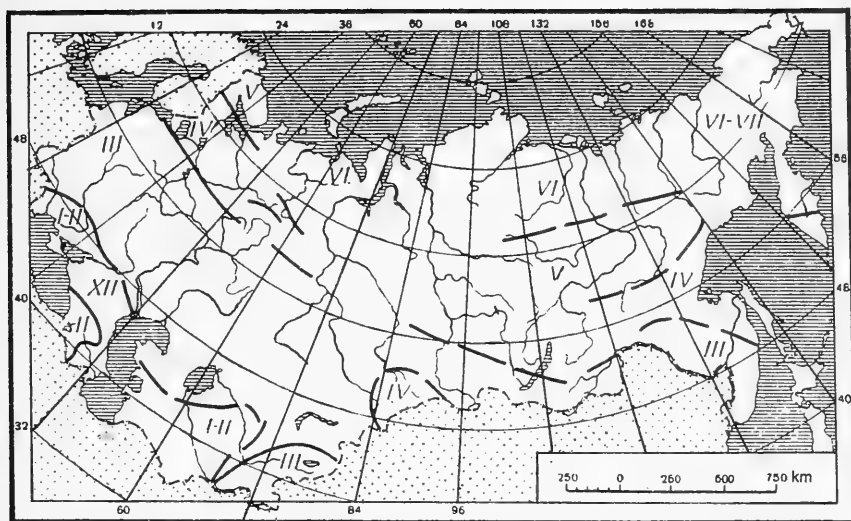


Fig. 135. The time of appearance of the earliest litters of fox cubs at the surface near burrows. Roman numerals indicate months (from Chirkova, 1960).

Fertility of the red fox is also geographically variable. The least number of young—an average of 3.5 up to 6—is observed in the Karelian ASSR; an average of 4.9 up to 8—in the deserts of Turkmen and Uzbek SSR, and up to 8–9—in high montane zones of the south. In the zone of the southern taiga and broad-leaved forests of the European territory of the Union, in the southern regions of Krasnoyarsk territory and in Buryat ASSR, a fox family has an average of 4.0–4.9 young. There is higher fertility in the Stavropol' steppes and western Siberia—5.0–5.6 on the average and up to 13 cubs (A.F. Chirkova). Fertility is high in the northern forest-steppe of Volzhsko-Kamsk territory: 5.8 on the average, maximum 13 (V.A. Popov).

There is great variation in time of reproduction of the red fox in one place in various years related to variation in food conditions (Fig. 133). Strong frosts and snowstorms delay estrus. The individual times of estrus and rut vary strongly depending upon age, growth conditions of the individuals in various fox generations, upon the course of female reproduction in preceding seasons, etc. Thus, in Kanino-Timansk tundra the time of rut in successive years differed by 1–5 months. Deviations in the time of beginning of estrus in the forest zone of the European territory of the USSR for a 3-year period constituted 3½ months. Judging by study of the reproductive organs of foxes obtained in winter, females in estrus condition might have

been found in this zone starting from January and even the end of December up to the middle of April. During successive years, the beginning of estrus was offset by 1–1.5 months. There were strong changes in intensiveness of rut. In favorable years, concerted estrus
 368 took place in the course of 1 month; in the unfavorable years, it expanded to 2½ months. In the Stavropol' steppes, the time of estrus is displaced in successive years by 2–3 months. The whole period of reproduction of red fox in each place from the beginning of rut to the appearance of fox cubs at the burrow is about 6 months, but even longer in the desert zone.

Fertility also changes annually; primarily, the quantity of reproducing males and females varies (Fig. 136). In years of good nutrition, 70–80% and up to 100% of females participate in reproduction; at that time, all den burrows are occupied and individual foxes deliver the young even outside them.

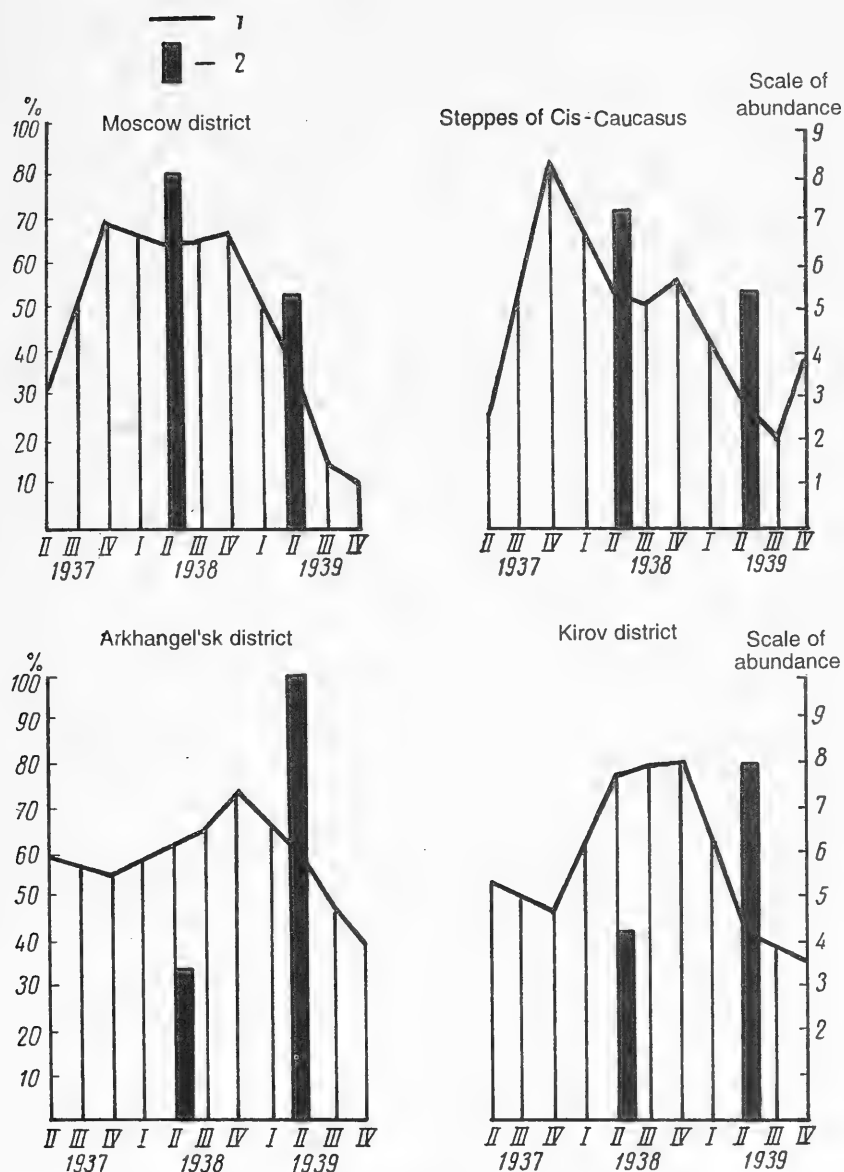
369 In an unfavorable year, up to 50–70% of females remain barren (did not come into estrus, not covered by males, with resorbed embryos and also aborted ones). The majority of den burrows at that time were empty. As a result, reproductive increase sharply decreased compared to the preceding year.

Reproduction of the various subspecies of red fox, especially in Siberia and montane places, has not been studied.

In Bulgaria, foxes reproduce at various times also. The rut of foxes in southern Bulgaria begins in January, and in northern Bulgaria—in February. The female fox gives birth to 4 to 9 and up to 12 young. In the USA the red fox gives birth to up to 10 cubs; on the average 5–6; in the eastern states, they are born at the end of March—the beginning of April; in the steppes of Oklahoma there are 3–9 cubs (Selko, Krefiting and Fletcher, 1942; Hamilton, 1943; Trippensee, 1953; Atanasov, 1958).

*Growth, development and molt*⁴⁵. Cubs are born blind, with closed ear pinnae and without teeth. Their body is covered with dark-brown fluffy fur. The tail is narrow at the tip, and in the majority of cases with fluffy white fur. The weight of the newborn wild fox cub is 56–110 g, averaging 86.9 g, on fur farms, 50–150 g, normally 80–100 g, body length about 14.5 cm, tail 7.5 cm. The cub's eyes open on the

⁴⁵In wild foxes, this aspect is insufficiently studied; therefore, separate indices are adopted from the practice of fur farming (Starkov, 1932; Bogolyubskii, 1939; Leshchinskaya, 1950; Il'ina, 1952; Ereemeeva, 1954).



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Fig. 136. Red fox reproduction in relation to the number of small rodents in various natural zones of the European part of the USSR (from Chirkova, 1947). 1—Number of small rodents in scale of abundance; 2—Percentage of females ready for reproduction from total number of investigated animals (laboratory analysis). On the abscissa, years divided into quarters.

13th–15th day on farms, at that time also the ear canal opens and teeth appear in the upper jaw and after about 3–4 days more, in the lower. At the age of 3–4 weeks, fox cubs in nature begin to come out from the burrow and are gradually schooled in different kinds of food, which is brought by the parents. The lactation period lasts about 6–7 weeks. The fox cubs are born short-legged, large-headed and with broad chest. Later, the extremities grow intensively, and in 3–4 months, the whelps are long-legged, narrow-chested and sinewy. Body proportions of the adult animals are attained at the age of 6–7 months.

Replacement of milk teeth by permanent ones in southern Ukraine takes place before the age of 4 months⁴⁶; in the middle of July, the dental formula of the young animals is the same as that of adults. Later, until age of maturity, only the canines obviously grow, and to the end of life, wear more quickly than other teeth. In contrast to the Arctic fox, tooth wear in young red foxes begins with the incisors of the lower jaw and with aging, it occurs in a definite succession. On this basis, it is possible to determine the age of foxes according to the condition of the teeth (Brauner, 1914; Grigor'ev and Popov, 1940, 1952; Smirnov, 1960).

In Kiev district, weight of wild fox cubs at about 1.5 months old is from 900 to 1350 g with body length of 36 cm, and the tail 13.5 cm; at 2.5 months—from 2 to 2.5 kg⁴⁷ with body length of 61–62 cm and tail 26–30 cm. In adult foxes and yearlings caught from November to February in the forest-steppe and steppe zone (especially the former), average body length reaches 72.1 cm and up to 89 cm⁴⁸, the weight of a carcass without skin averages 4.4 kg, reaching 8 kg⁴⁹ (A.F. Chirkova).

The life duration of the red fox in captivity is up to 25 years. In nature, foxes live for only a few years, usually not more than six.

The development of the pelage was studied in the silvery-black foxes on farms near Moscow (Leshchinskaya, 1950; Eremeeva, 1954).

⁴⁶On farms, the replacement of incisors in the fox takes place on the 90th–105th day; after this, during the course of up to 150 days, the canines and premolars are replaced.

⁴⁷On farms the average weight of a month-old fox cub is 700–750 g and after that the monthly weight increment is about 1 kg.

⁴⁸Utilizing measurements of more than 2,000 foxes from all zones of the Soviet Union.

⁴⁹The fresh skin of a red fox weights 500–600 g.

The formation of hairs already proceeds in embryos and in them the first hairs appear on the nape on the 41st day of pregnancy. The shedding of hair of the first coat takes place in foxes beginning with the 35th and up to the 75th–80th day of life; the guard hairs are lost first, the underfur by the 110th–120th day, in August–beginning of September. Intensive shedding of guard hairs of the juvenile coat is observed in the second half of August, irrespective of the time of birth. In August, vigorous development of the hairs of the first winter (adult) coat begins; its main mass matures at the beginning of December.

In the adult silver-black foxes, molt takes place twice a year. The spring begins in February, and complete shedding of winter pelage occurs from March until July; growth of the new proceeds simultaneously. Pelage replacement begins in the pregnant females, after that in barren ones, then males, and last of all in old individuals. Early growth of the winter hair becomes obvious from August on, and proceeds until the beginning of November, when it ends in full development of the winter fur. Maturation of the fur in a warm autumn is delayed for 1 to 2 weeks; with an early frost, it is accelerated.

In nature, the timing of molt and of juvenile hair in the red fox change depending upon latitude and longitude of the location, nutritional and meteorological conditions, sex, age and condition of health. The more northern and eastern the place, the later molt begins in spring, and the earlier the maturation of winter fur occurs. In the temperate zone (in the plains), molt of the fox begins in February–March, but in the southern deserts, even earlier, proceeding vigorously in April–May and lasting until the middle of summer; in the north of western Siberia (in Yamalo-Nenetsk Nats. Region), from end of March–beginning of April. In montane regions, it is delayed; in Armenia, molting foxes were repeatedly observed in July and even at the beginning of August (Dal', 1944, 1948b, 1949; Rakhmanin, 1959). Growth of winter fur in the deserts begins in July, and by December foxes are clothed in dense winter fur (Turkmeniya; Shcherbina, 1961a). Maturation of the winter fur of the red fox in other zones takes place in the course of November and December. In different years, incomplete pelage growth is observed in January and even later; some foxes in these years simply never acquire complete winter fur.

Enemies, diseases, parasites, mortality and competitors. The enemies of the red fox are not numerous. Of mammals, the wolf represents the greatest danger, lynx and wolverine considerably less,

and among birds, the large raptors—eagles and sea-eagles (about 1% occurrence in castings; Gusev and Chueva, 1951; A. Popov, 1954). In the Cis-Caucasus, the imperial eagle and fox mutually harm each other—the eagle sometimes preys on the fox and the fox destroys its eggs.

The majority of diseases of the fox have not been studied in nature. Nonetheless, from time to time disease breaks out among foxes, causing massive mortality. They are connected with deterioration of feeding conditions, mainly disappearance of small rodents. Food scarcity is accompanied by the emaciation of mature adults and promotes the appearance of outbreaks of various diseases. Some red fox diseases are, probably, common to the small rodents on which this animal feeds, as well as to other animals. Disease transmission is favored by high density of the fox population and the behavior of hungry animals (frequent biting of one other, cannibalism).

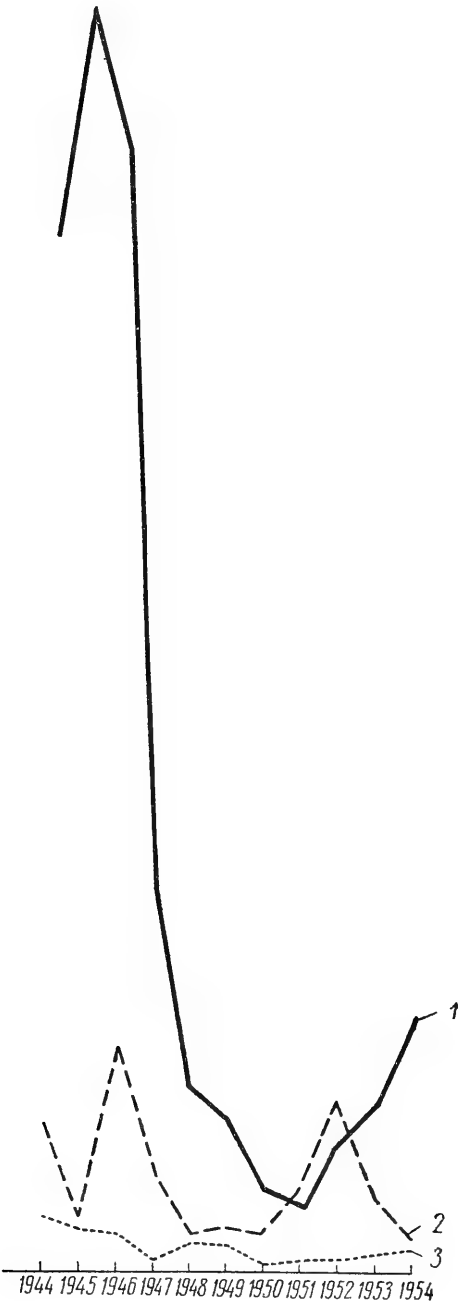
High mortality among foxes was recorded during the mid-30's, 40's, and mid-50's of our century. The plague is expressed most sharply in places with high population density—in the steppe and semidesert zones of the European part of the USSR. Individual hunters found there tens of fox carcasses, and many diseased foxes. An especially severe epizootic and mass mortality of foxes appeared in 1944–1947 in the European territory of the USSR, in the Caucasus and in Kamchatka, and to a lesser extent—in Yakutiya, western Siberia and the Altai, when mass reproduction of small rodents, followed by their disappearance led to starvation and the outbreak of disease among red foxes. In silver-black foxes on fur farms, a great number of diseases were revealed. It is necessary to realize that wild foxes are included in the chain of many infectious diseases of animals and human.

- 371 Among wild foxes in the USSR, rabies is widespread, occurring in all natural zones and especially often appearing in the mid 1940's in the territory of the European part of the USSR. The disease also was recorded in many foreign countries. In the USA, of hundreds of foxes caught in an infected region, the infection rate of rabies was 3.1 to 5.8%. In the extreme north of Arkhangel'sk district, carnivore distemper—a neuroviral disease—manifested itself among foxes in extreme northeastern Siberia, and particularly sharply in Kamchatka; it already was known early in the first quarter of the past century. In the tundras of Arkhangel'sk district, the Arctic fox is the main virus vector. In years of outbreaks, up to 20% of the red foxes are virus vectors.

Carnivore plague appeared chiefly in the steppe zone and sometimes caused general epidemics. In individual cases, epizootic jaundice (leptospirosis) and tularemia were revealed, but foxes are not very susceptible to becoming ill with the latter. Foxes may also become sick with listerellosis and spirochetosis, and act as vectors in the spread of erysipelas infection, brucellosis and tick-born encephalitis (Sokol'nikov, 1927; Chirkova, 1941, 1952; Isakov, 1949; Pavlov, 1953; Vyshel'skii, 1954; Dunaeva, 1954; Sludskii, 1954; Kantorovich, 1956, 1956a, 1963; Rementsova et al., 1956; Galuzo, 1957; Karochevskaya, 1958; Tirkel', 1958; Bindrich et al., 1959; Wood [and] Davis, 1959; Ismagilov, 1961; Morozov, 1961).

A disease of unknown etiology and mortality among foxes and other carnivores took place in the region of Lake Sartlan in Novosibirsk district, due, as was supposed to poisoning by toxic substances leaching from the ground, but this was also disputed (Berman and Strusevich, 1957). The possibility was considered of it being due to an acute form of encephalomyelitis which was observed in silver-black foxes (especially young) in nurseries (Isakov, 1945; Vyshel'skii, 1954). In individual cases, the infection of foxes with plague (*Bacillus pestis*; Rall', 1958) was observed. In some years the foxes are
 372 found to be infected with large quantities of fleas and ticks, especially in the desert and steppe zones; many species of these ectoparasites serve as carriers or transmitters of dangerous infections of humans and domestic animals.

The itch mite *Sarcoptes scabiei* induces mange in foxes. In the extreme form in which this disease appears, the body of the fox becomes almost naked and covered with hemorrhagic scabs; such
 373 animals gradually die. Mange on foxes in the USSR has been known since 1919 (Chirkova, 1957). It first appeared in the form of several foci in the southwestern Ukraine, and then spread over a vast territory (Fig. 138). At the present time mange is established in foxes of the steppe, forest-steppe and southern forest belts of the European part of the USSR eastward to the Volga and even beyond. The spread of mange is favored by temperate, warm and humid climate; fox burrows in the above-mentioned zones are a very favorable microclimate where itch mites and their eggs are preserved for a long time. Evidence of disease and death of red foxes from mange in the forest-steppe and steppe belts of the European part of the USSR comprise 55% of all known cases of disease and death among foxes of these zones, averaged over many years.



Endoparasites of wild red foxes have not been sufficiently studied (Petrov, 1941, 1958; Chirkova, 1948; Evdokimova, 1954; Troitskaya, 1955; I. Romanov, 1956). On fur farms of the USSR, up to 60, and in nature more than 20 helminth species are found in red foxes and several species of coccidians of the genera *Izospora* and *Eimeria*. The richest helminth fauna of foxes is in the forest-steppe and the northern belt of the steppe zone, while the poorest is in the desert zone. Infection in the fox population is almost 100% everywhere; only in some places and in some years does it decrease.

The nematodes most frequently found in wild foxes are *Toxocara canis*, *Toxascaris leonina* and *Uncinaria stenocephala*, found in the gastrointestinal tract, and *Thominx aerophilus* and *Crenosoma vulpis*—in the lungs. Among trematodes, *Alaria alata* is most often found, among cestodes, *Taenia pisiformis* and *Mesocestoides lineatus*; and of acanthocephalans, *Macrocanthorhynchus catulinus*—all in the intestinal tract. The degree of infection with various species of helminths changes not only by territory but also annually. Species specificity has been recorded for some zones. The alveolar echinococcus, *Alveococcus multilocularis*, and the trichinellid *Trichinella spiralis* are especially dangerous, as is *Dracunculus medinensis*, the liver fluke (*Opisthorchis felineus*) and certain tapeworm species (*Diphylidium caninum* and *Diphylobothrium latum*); they are transmitted to humans, and some species are also characteristic of domestic animals.

Echinococcosis and trichinellosis are widely distributed infections among wild foxes. Echinococcus infection is known in red foxes of all natural zones of the Soviet Union. High infection rates were observed in Alma-Atinsk district (25% of carcasses examined), in Kamchatka (30.5%), in Omsk district (up to 35%) and in Krasnoyarsk territory (average of 55.9%, and in some steppe regions, up to 70% in individual months) (Kadenatsii, 1953, 1959; I. Romanov, 1958; Kozlov, 1961, 1962; Arslanova, 1962). In different cantons of Switzerland and northward, 36–40% of foxes are infected with echinococcus (Vogel, 1955, 1960).*

*In Russian original, misspelled Fogel'—Sci. Ed.

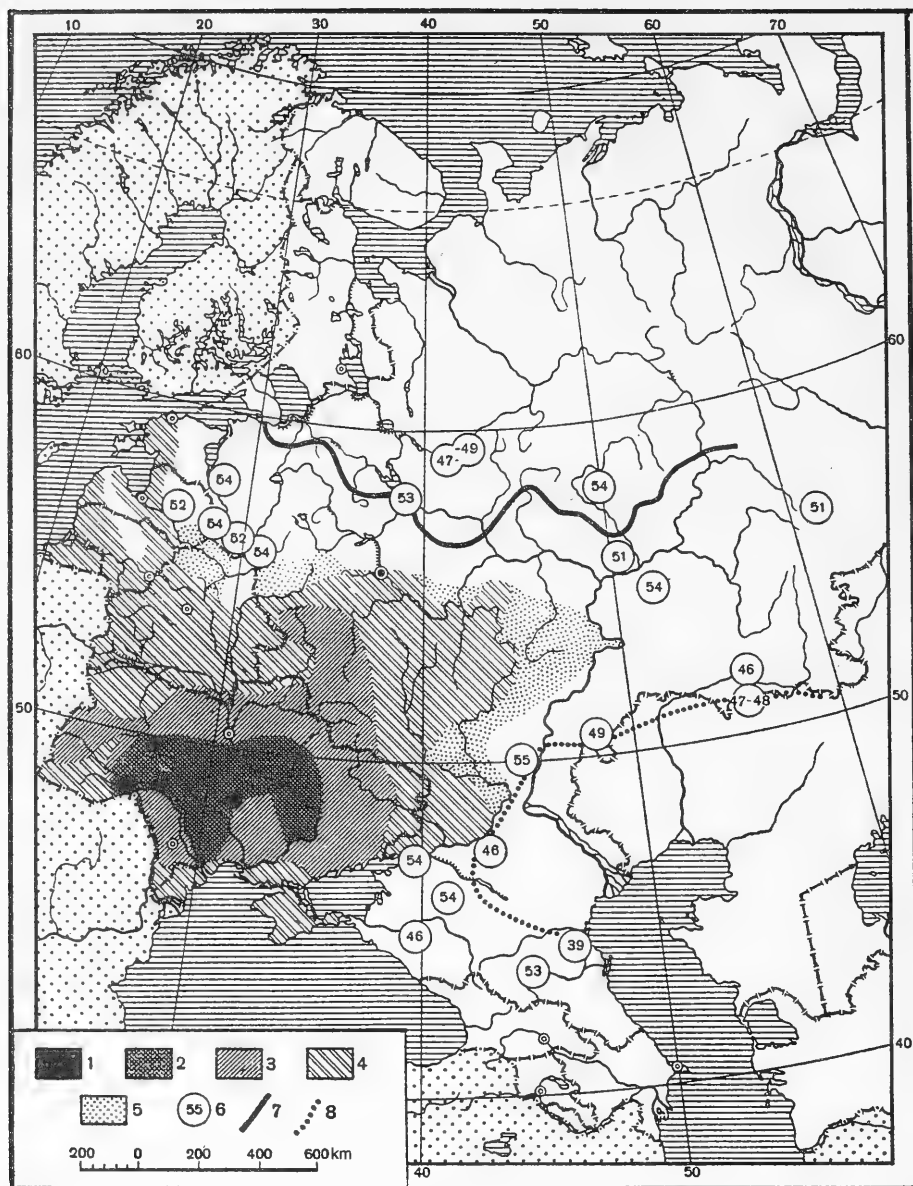


Fig. 138. Distribution of itch mite-caused mange in red fox for 1919–1954 (from Chirkova, 1957, simplified). 1—Primary foci of mange in 1919–1922; 2—infected area in 1923–1933; 3—same in 1934–1940; 4—same in 1945–1949; 5—same in 1950–1954; 6—Points of disease isolated from general area of the epizootic; the year is indicated in circles; 7—southern boundaries of taiga forest; 8—boundary between steppes and semideserts.

Trichinellosis in foxes is known from individual cases of infection in Omsk district, 3.8% in Stavropol', up to 11.1–21.7% in Khabarovsk territory and Kamchatka, 12.3% in Tatarsiya, from 0 to 12.5% (in various years) in the northern forest areas of the European part of the Soviet Union, and up to 20.8[%] in the central forest regions, 36.4% in Saratov district, 42–54% in Belovezhsk. Forest, 56.5% in the Crimea, and up to 74.7% in Bashkiriya (Kadenatsii, 1953, 1957; Mashirov, 1955; Tret'yakova, 1956; Belyaeva, 1957; Kozlov and Kontrimavichus, 1961 (1962); A.F. Chirkova).

Many helminth species common to other carnivores are found in foxes, in particular, with domestic animals, a fact which is exemplified in the Crimean fox (Table 44).

Among other important mortality factors of red foxes are forest fires, burning in steppes and in reed thickets, heavy downpours in the south, especially in the mountains, deep snowfall in deserts and mountains, flooding on flood plains of large rivers, and the accumulation of oil in the regions of oil extraction. Mortality due to elemental calamities was observed in 2 to 16% of all cases, occurring particularly often in deserts. Foxes also die from poisoned bait scattered for control of small rodents, as was recorded in 4–14% of cases, more often in the forest zone and in the mountains.

Competitors of foxes for food are all species of small carnivores, especially those belonging to the family Mustelidae and species of the family Canidae. The red fox sometimes occupies burrows of the Arctic fox. However, here the significance of foxes as competitors (Skrobov, 1958, 1960, 1960a) is greatly exaggerated, since the fox in the denning season selects biotopes which are not characteristic for Arctic fox, mainly forested river banks with drier and lighter soils. The red fox, in contrast to the Arctic fox, prefers to feed on rodents of the genus *Microtus*. In the zone of contact of both species in the tundra, the red fox is not numerous.

In forest and steppe zones, the fox competes with the badger, whose burrows it often occupies; in steppes, the fox occasionally lives in the burrows of corsac fox and marmot, and in the desert—in wolf and porcupine [burrows] and in colonies of gerbils; in the Caucasus mountains, the burrows of foxes are occupied by the forest wild cat *Felis silvestris*; in Tadzhikistan, the steppe cat [*F. libyca*] is a competitor of the fox. Death of red foxes due to encounters with carnivores and competitors constitutes 2–12% of the total number of deaths (more often in forest and desert zones).

Table 44. The ratio of species-specific to generalist helminth species in the foxes in the Crimea (from Kadenatsii, 1957)

Total helminth species	Species- specific	In common with other species				
		With dogs	With cats	With badger	With steppe polecat	With beech marten
34	$\frac{4^{50}}{11.7}$	$\frac{29}{88.5}$	$\frac{12}{35.2}$	$\frac{8}{23.5}$	None	$\frac{2}{5.9}$

Population dynamics. Numbers of the red fox are not stable (Formozov, 1935; Chirkova, 1941, 1947, 1947a, 1952a, 1953, 1954; Teplov, 1949, 1960; Shcherbina, 1961). In favorable years, minimal density of the fox population occurs in spring after the end of the harvest. A maximum number is attained with the conclusion of reproduction and is usually observed in autumn after the emergence of the fox cubs from the burrow. Rarely is the increase in the population more than 3–4 fold (taking an average in such years of 7 to 8 cubs in a litter). In unfavorable years, especially with an epizootic outbreak, the foxes which remain until spring, with worsening conditions, produce a few weak offspring which soon die. In this case, the population in autumn may display even fewer numbers than in spring.

The multiannual numerical dynamics of the red fox are reflected by the well-known data on tanned skins. Tanned skins of red fox has changed within three-fold limits from the middle of the 20's to the 50's of the twentieth century]. The rise in number of foxes took place in the mid-20's and 30's. The minimum number and weak harvest arrived at the beginning of the 30's. Unusual abundance of foxes was observed in time of war—in the mid 40's, when, beginning with 1942/43, tanning quickly grew until 1946/47, after which it decreased. A new increase was noted at the beginning of the 50's. During the post-war period, tanning of red foxes increased by 150% as compared with the prewar years. The increase in tanning was promoted not only by the general growth of the fox population in all natural zones of the country, but also by intensification of harvest (Fig. 140).

⁵⁰In the numerator—number of helminth species; in the denominator—percentage of generalist helminth species of a given domestic form.

375 Near the northern limits of the range, fox populations vary quite sharply every 2–4 years, following the fluctuations in numbers of small rodents. In the Nenetsk National Region, tanning of fox skin usually grows in the course of 1–3 years and sharply decreases in one year; often, they co-decline with the dynamics in Arctic fox numbers. On the Kola Peninsula, the numbers of red foxes depend upon mass reproduction of red-backed voles, which is repeated nearly every 4 years (Koshkina, 1957; A.F. Chirkova).

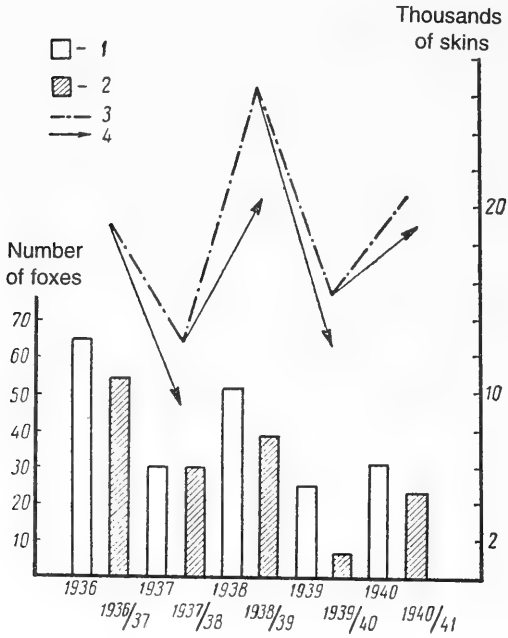
In the taiga zone in the northeastern European territory of the Union, in the Pri-Yenisei taiga and in Yakutiya, red fox numbers depend on reproduction of arctic hares (Middendorf, 1853; Teplov, 1949; S. Naumov and Popov, 1957). In Yakutiya, the fox populations quickly increase in years of "outbreak" of this rodent*, in the 2nd–4th year after its mass reproduction. The increase is repeated after 8–12 years, not synchronously in various regions of Yakutiya (Labutin, 1960). In several regions of the north, there is a significant abundance of forest game birds. In the forest zone, the peak in fox numbers occurs in years of decrease in number of hares and game birds, coinciding with reproduction of small rodents. Under such conditions, for example in 1943/44, tanning of fox skins in Yakutiya increased by 310%, attaining in 1944/45 22.8 thousand items, while the usual increase did not exceed 200% and the average number of tanned [skins] per year (for 34 years) consisted of 5.8 thousand items. In the Nizhne-Kolymsk region, from 20 to 700 skins of fox were tanned in various years; the annual catch of foxes increased sometimes by 3–4 times. In Pechoro-Ilychsk preserve, fox numbers changed 8–12 fold in the course of several years (Teplov, 1949). In Tatar Republic, 5 increases in fox numbers were observed in the last 40 years, at intervals of 7 to 9 years (V.A. Popov). In the Far East, growth of fox numbers is connected with the migration of spawning salmon into the rivers, which usually occurs biennially, as well as on the abundance of small rodents; other kinds of food are also significant (A.F. Chirkova).

In the forest-steppe and steppe zone, the dependence of fox numbers upon small rodents, mainly the common [*M. arvalis*] and social [*M. socialis*] voles and sagebrush voles [*Lagurus*] is precisely evident. Tanning of red fox skins in successive years increased by 300 to 400% in the Altai territory and Penzensk district, by more than

**Sic*; hares are no longer considered rodents, but lagomorphs—Sci. Ed.

400% in Saratov district and Stavropol' territory, and by 520% in Rostov district. During the extent of the postwar years, tanning varied in Voronezh and Volgograd districts 6-fold and in Rostov district—10-fold. In 1956/57, as a result of food shortages, tanning of red foxes in Orenburg territory decreased 10 times. On experimental areas in 376 Kiev and Voronezh districts and in Stavropol' territory, the number of foxes changed 3–4 times in two successive years.

In the southern deserts of Kazakhstan and in Middle Asia, red fox numbers changes during a 2–4-year period, depending mainly upon reproduction of several species of gerbils and voles. Peaks of skin tanning are repeated here about every decade. The amplitude of



375 Fig. 139. Counts of red fox in an experimental plot, prognosis of numbers and general catch (tanned skins) around Stavropol' territory, Cis-Caucasian steppes (from Chirkova, 1947). 1—Number of foxes by count of litters in spring; 2—Fox catch in experimental plot; 3—Tanned skin in the territory; 4—Prognosis of numbers in the direction of forecast decrease or increase of population. Left—number of established individuals according to No. 1. Right—thousand skins.

fluctuations in tanning in Turkmeniya and the Uzbek SSR changed not more than 2 times during the postwar years. In montane regions of the south, red fox numbers change depending on the reproduction of montane voles. In Armenia, the Tien Shan and the Pamir, fluctuations in fox numbers is frequent but within a small range, which corresponds to variation in populations of mouse-like rodent. In Tadzhikistan and Kirgiziya, tanning in the postwar years fluctuated 2 times; in Dagestan, 2–3; and in Armenia, 3–3.5 times (A.F. Chirkova).

The influence of harvest on the dynamics of fox numbers has been little studied. This effect depends on the number of hunters, the time of harvest and the instruments of capture employed. On an experimental area in the former Spitsevs'k region of Stavropol' territory, hunters each year caught from 24 to 100% (average, 78%) of the counted fox population. In Brovsk region of Kiev district, on a permanent plot of 400 km², 53.5% of the foxes counted in summer were caught in the winter of 1951/52. Catch of foxes within this limit does not, apparently, undermine the main parent population. Only in 1954 and 1955, after a heavy winter in Stavropol', was there observed a considerable decrease in the fox population, harvest sharply decreased, and starting from the middle of winter, capture of fox was prohibited in 12 regions of the territory; after this the population of animals was again quickly restored. An analogous case of overharvesting took place in Yakutiya in the beginning of the 50's;

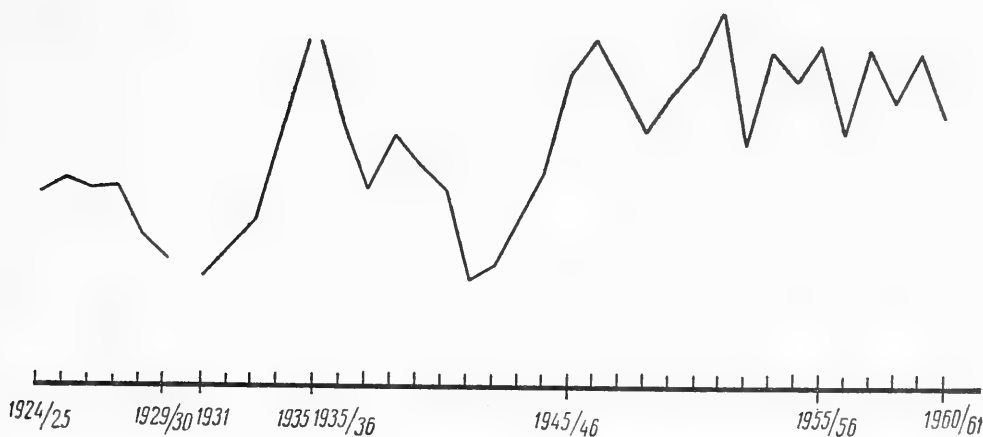


Fig. 140. Fluctuation in tanned skins of red fox within the whole Soviet Union as an indicator of the fluctuation in numbers of the animal (A.F. Chirkova).

after a temporary prohibition on capture, in the 3rd year tanning again regained its usual level (A.F. Chirkova).

The abundance of the red fox, which was evidenced everywhere in postwar times, is explained both by mass reproduction of small rodents, and also by the absence of regular harvesting.

Field characteristics. Tracks of red foxes are characteristic and easily distinguished from those of related species. The gait of foxes is direct (straight as a string) alternating footprints. In an easy trot or "trusts [jog-trot]" by which the red fox most often moves, it places its anterior left foot and the posterior right exactly in one place, and then, stepping forward with the right anterior one, it lowers in its place the left posterior foot. In this way the impression is given that a bipedal animal has passed by. The distance between footprints is 20 to 30 cm. With a slower gait, when the fox sneaks up on its prey, looks out for danger, or satiated, leaves its food for a rest, the distance between tracks decreases until they nearly contact and the track of the hind foot is slightly behind that of the forefoot. When excited or disturbed, the red fox proceeds in large bounds. In deep snow, it moves in a short gallop, in which the tracks of all four feet remain. Running from danger, it careers in an extended gallop. In this case, it can make a jump of up to 4.3 m (Dinnik, 1914) (Fig. 143).

The footprint of the red fox is similar to that of the dog, but more compressed, narrow and, not as wide-pawed; the contours of the lateral digits do not touch the posterior margin of the middle digits and do not cover them from the sides as in dogs. On a thin layer of soft snow or on wet soil, the prints of the claws are always visible. Measurements of the elongated track of the foot are $4-5 \times 6-7$ cm with claws (Fig. 142). Loading on 1 cm^2 of the track surface is 40 g or more in the middle belt [of the Union] and 28 g in the Pechora [region] (Formozov, 1959; Teplov, 1960).

The female track is smaller, narrower and more pointed and the stride is shorter; in young, the tracks are still smaller and not so well marked as in females. Anterior drag marks and posterior drag-marks on the snow made by the shorter-legged female are, naturally, more frequent and longer. The female often proceeds by hiding behind bushes and irregular relief while the male usually walks directly forward, not hiding. In time of rut, the female leads the males. The sex of foxes can be determined by the manner of urination; with males usually urinating near protruding objects—rocks, hummocks or bushes.



Fig. 141. Track of red fox crossing a marsh in snow of moderate depth with heavy frost. Oka preserve, Ryazan district. January 1950. Photograph by V.G. Heptner.

According to hunters of East Siberia, tracks of melanistic individuals, especially blackish-brown foxes, by comparison with red are differentiated by their larger dimensions, not only due to the larger size of the feet, but also by their greater fluffiness. Melanistic foxes are more cautious than red (Slyunin, 1900; Buturlin, 1913). Hunters consider that the better furred the fox, the more frequent are its tracks. Individual differences in tracks exist, for example, "*lapistost*"*

*An uncommonly used trapper's term—Sci. Ed.

when the heavily furred pads of the feet leave a wide and diffused track.

The direction of the paths of a fox on the deep or drifted snow can be determined by the drag marks. The latter, produced when the foot is raised from the track is usually shorter and more abruptly
 378 lifted from the snow, breaking its edge; snow pellets are thrown forward. The drag mark formed while setting the foot onto the snow is elongated and sloping.

A series of fox tracks extends in a patterned manner, traversing a field, meadow, or shrubland, passing through hills, descending into a ravine, following the edge of a wood, sometimes along ski-tracks, often with stops along the way. During times of food-seeking, the fox walks in a zigzag manner, moving first to one, then the other side, examining each hummock, clump of grass, and bush met with, walking around haystacks and dung-heaps, and not neglecting a single object on the snow surface in its way, sometimes returning along its own tracks. The red fox does not make trails, since on passing for a second time or repeatedly along its tracks, it places its feet accurately in the place of the previous tracks. Trails are made only by young foxes, usually along banks of small creeks overgrown with reeds. At different times of day, the red fox traverses particular paths and on bright days it hides more often than on cloudy ones.

In years with abundant small rodents, on the path of the well-fed fox, holes are left in the snow through which it hunted voles. In deep snow, these "kopka" [diggings] are up to 80 cm deep (Lapland preserve; Nasimovich, 1948). On a 2-km path up to 30 holes were found (Formozov, 1959). Along the tracks of foxes, killed and mauled shrews and even moles, which it usually does not eat, are often found. Shells of eggs, sucked in summer and rotten in winter, have two holes made by the canines of the fox at a distance of 1.5 cm from each other. The remains of a large or moderate-size bird are usually encountered in the form of the whole wings or separate remiges or tail feathers, with the quills severed at the base. The red fox, upon capturing a hare, usually does not completely eat it, but digging a hole in the ground or snow, puts the remaining part of the carcass there and treads and kneads the surface with feet and nose.

The lair of the fox is found sometimes under a bush, or near a hummock, often on its summit, on a haystack or thatch pile, and even on a bent tree at a height of some meters from the ground. In forested localities, the red fox prefers for resting coniferous forests—spruce

forest, where it can hide among the shaggy boughs, pine forests with mossy bogs where it can hide behind hillocks. From one lair to another, tracks of the fox may extend for some kilometers. Sometimes, before retiring to rest, the fox executes a trick—a sideways jump into any sort of shelter. The dimensions of the lair in the Lapland preserve are 40×50 cm in width and 10 to 15 cm in depth (Nasimovich, 1948).

Except at the breeding period, red foxes rarely frequent burrows; only in extreme cases, in times of wet weather, during severe frosts, or when hiding from danger, does the fox enter a burrow.

In the second half of winter, paired tracks of foxes are often encountered, and at time of estrus, straight away several animals are together. With this, one may observe the signs of fights among males, and remains on the snow of tufts of hair, even clots of blood. In spring, sticky secretions may be found on the tracks, characteristic of estrus, and in years with food deprivation and at the beginning of epidemics, bloody mucus may be found.

379 Feces are usually 1.5–2 cm thick and 3–9 cm long, closely covered with a film of mucus and well-formed, sometimes with a constriction; in fresh form dark-olive in color, and on drying—whitish and earthy. More often, it consists of fur of rodents, sometimes with a mixture of small feathers, large hairs of domestic animals, pieces of bones, parts of insect chitin, fragments of dry plants and



378 Fig. 142. Track of red fox on clay soil. Manych. 28 May 1940. Sketch by A.F. Chirkova, natural size.

others. In summer, especially with small numbers of rodents, feces are met with that are entirely composed of chitinous parts of insects, which fall apart in the hand. In the floodplains of the Volga and Kama, with insufficient animal food, foxes in winter eat rose-hips and their excrement then has a brick-red color (V.A. Popov). Near the den burrow, at points around the main entrance, is scattered excrement of the fox cubs, 8 to 15 mm thick, depending upon age and sex. Here also occur the discarded remains of prey brought by the [parent] foxes. Narrow paths lead from the den burrow, which the fox



Fig. 143. Different gaits of the red fox (from Korneev, 1956): 1—Walking, light trot; 2—extended trot; 3—trot with "paired limbs" [pacing ?]; 4—gallop.

cubs trample out on various sides. On these as well, one may find pieces of feces and remains of the fox cubs' food.

The red fox orients itself by sound; it can hear the sound of blackcock changing roosts at about 600 paces, the flight of a crow—at 1/4 to 1/2 km and the squeak of a mouse—at around 100 meters (Zvorykin, 1931). But cases of completely deaf foxes are known in
 380 nature (Postnikov, 1936). Sight in the fox is well developed, but it reacts mainly to moving objects. Scent is good, but weaker than in specialized dogs. Apparently, olfaction operates at close range. The fox shifts objects along the ground not only by its feet but also its muzzle.

The voice of the red fox may be heard before storms, in inclement weather, and severe frosts, but most often at the beginning of the breeding period, when the female calls males by barking; usually at the beginning of twilight and until morning (p. 532). After 2–3 dull, metallic barks resembling the voice of small mongrel, comes a short monotonous howl. The female barks while sitting, raising its muzzle upwards. Males do not respond immediately: their barking is more frequent and impatient and is interrupted not by howling, but by a yelping sound resembling the cry of a jay or fighting cats (A. Ch.).

Practical Significance⁵¹

The red fox is a valuable fur-bearing animal. In the past century, more than one hundred thousand foxes were caught annually in Russia. In the beginning of the twentieth century (1907–1909), according to data of the International Fur Trade, the yield from fur bazaars in Russia was 363 thousand red fox skins including *sivodushka*, *chernoburaya* and *karaganka* foxes.

In the Soviet Union, from 1924/25 to 1958/59, an average of 487.3 thousand red foxes were caught yearly. During the post-war years, tanning considerably increased. During a 35-year period, about 17 million skins were prepared. In fur manufacture, red fox occupies fourth place. The greatest number of skins tanned are from steppe and desert regions; at the same time, the taiga zone yields more costly fox fur of better quality. One hunter in the forest zone frequently catches only occasional animals, rarely more than ten, while in the

⁵¹Silant'ev, 1898; Brass, 1925; Brauner, 1930; Chirkova, 1941, 1948, 1963; Korneev, 1956; Ling, 1956.

steppes and deserts, he gets several tens and in some years, even hundreds of foxes.

The fox destroys harmful rodents—voles, mice, ground squirrels, hamsters and others, which has especially great importance in agricultural regions. Eating about 300 g of meat per day, each fox can destroy about fifteen voles⁵² and in one year not less than 3000 voles and mice, or 1000 gerbils. During the three summer months, one red fox together with its litter can destroy more than 500 ground squirrels. It destroys also poisonous snakes. Among insects sometimes eaten by the fox when abundant, especially in steppes, deserts and montane regions of the south, the majority are locusts, termites, cockchafer beetles, weevils, darkling [tenebrionid] beetles, larvae of beetles and moths which belong to the pests of agriculture, fruit orchards and forestry. In southern Turkmeniya, analysis of animal food of the fox characterizes it as an unquestionably useful animal (Table 45).

In the period of low numbers of small rodents, the fox destroys many more than in times of abundance. Therefore the value of fox as a destroyer of agriculture pests is especially great in the years of their depression, since it hinders the quick restoration of their numbers.

Accused as a predator, the fox is implicated in the destruction of game and song birds, hares, muskrats and the young of ungulates. The harm caused by this predator is especially appreciable in preserves, reserves, and hunting farms where game birds such as pheasants, partridges, grouse and others, which are ground nesters, are protected and raised, as well as in the neighborhood of poultry farms. However, often the charge of game destruction is exaggerated, 381 since the degree of fox damage is usually determined by the remains of food found at its burrow. The limb bones of hares or the wings of large birds may be preserved for a long time leading the observer into error. Thus, in North America, where rabbits (*Sylvilagus*) smaller than our species of hares are often eaten by red foxes, the remains of the comparatively large animals (piglets, hares, pheasants and domestic chickens) were found near burrows 11 times more often than in the excrement, while the remains of the meadow vole [*M. pennsylvanicus*] were found 75 times less often (Errington, 1935). It is also known that single individuals or separate litters of fox

⁵²In the stomachs of fox, up to 20–21 voles which it feasted on in a nest, were found (Formozov and Osmolovskaya, 1963).

specialize in eating several species of secondary importance, as for instance, domestic fowl (Pavlov et al., 1961; Ishunin, 1962).

The fox captures relatively few brown hares [*L. europaeus*] and destroys arctic [*L. arcticus*] and tolai [*L. tolai*] hares in considerable numbers only in years of massive diseases and plagues of these lagomorphs*. In Yakutiya where hares are characterized by sudden increase in numbers in the course of 2–3 years and also sharp decreases, these carnivores are not the cause of the periodic decrease in the number of hares, since its population in years of abundance of these lagomorphs* is insignificant. When signs of depression appear in hare populations, and epizootics develop, fox feed freely on them (more than 50%, and up to 96% of occurrences in the food of individual litters), and so do the majority of predatory animals and birds. Under these circumstances, the red fox serves as a factor of great importance in the sense that it rapidly removes carcasses of dead hares. Later, in the period of minimal numbers of hares, the fox as well as other predators, holds back a new wave in the growth of population of these lagomorphs* (Labutin, 1960). In some regions, the red fox kills many young ungulates, for example roe deer in preserves in Crimean region, but it destroys mainly weakened young, thus itself increasing the health of the population. The role of the red fox in destruction of small song birds is not great.

On the negative side, there is the role of fox in the transmission of several dangerous infections, especially rabies as well as carnivore distemper, wild rabies in the north, and several other diseases. The significance of the species in this respect is still not sufficiently studied. The fox is also dangerous as a vector of several species of helminths—alveolar echinococcus, trichina, tapeworms and others, as well as ectoparasites—mange mite, fleas and ixodoid mites—carriers of blood parasites and other infectious diseases of humans and domestic animals.

382 Techniques of catching the red fox are of various forms (Silant'ev, 1898; Sabaneev, 1904; Zvorykin, 1935; Chirkova, 1945; Gerasimov, 1950 and others), but basically in the greater part of the Union, it is trapped and shot. Methods and manner of setting traps in fox trails, in the places where it catches its food, in hare trails, and in deep snow—under the track; under ski or sled tracks where the fox is not afraid to walk along them—are exceedingly variable. Traps are also

*In Russian original, "rodents"—Sci. Ed.

Table 45. Correlation of vertebrate and invertebrate animals having different economic significance in the food of Badkhyz foxes (according to multiyear data; Shcherbina, 1961a)

Economic importance	Vertebrates		Invertebrates	
	Absolute number	%	Absolute number	%
Useful	799	21.3	731	11.6
Neutral	12	0.3	4	0.06
Harmful	2687	71.7	5549	88.3
Unknown economic importance	253	6.7	—	—
Total	3751	100.0	6284	100.0

set making use of peculiarities of relief and landscape—near rocks, lone standing trees, bushes, etc., on sites of old campfires, and near frozen sections of creeks and small rivers, where the fox crosses them. When a fox as determined by its track is found in a burrow, the trap is set at the hole. Traps are also set out near baits, in particular odiferous ones; sometimes live baits in the form of a small bird or mouse are used with them. A better method of setting traps is at lures*. On the tributaries of the Ob' [river], traps are placed near unfrozen parts of the river. In the south, traps are situated in former livestock corrals, and in the sand of southern Kazakhstan and Middle Asia—under bushes and under the nests of raptors.

Red foxes are ambushed at lures, by preparing in advance a place for sitting or a dug-out. They are hunted with a decoy mouse squeak or the cry of an injured hare. Hunting fox by beaters with flags is widespread. At the time of estrus, males are driven out and shot. In the forest zone, stalking is employed. In the south, they are hunted with guns along *chernotrop*** among the furrows of ploughed fields, where foxes like to mouse, and also in drives, the foxes being forced out from reed thickets of the steppe rivers. Hunting with hounds is widespread; it is only possible before deep snowfall, and is successful in places with varied landscape. Foxes are hunted by setting fox-terriers and dachshunds on them in burrows. A specific kind of fox

*The distinction between the Russian words "primanka—bait," and "privad—lure," is not clear in this context—Sci. Ed.

**Literally, "black path"; refers to bare ground in winter—Sci. Ed.

hunt is found in the steppes and semideserts of Kazakhstan and Middle Asia, with golden eagles and borzoi ("*tazy*"). In the Trans-Baikal steppes, foxes are hunted by driving them with horses.

In the greater part of the territory of the Soviet Union, the red fox, as well as other commercial species, is protected. Protective measures for the fox mainly include timing of the hunt, which is permitted only in winter. Harvest usually begins in November and continues to the end of February. Hunting seasons change depending upon the latitude of locality, and annually depends for its timing on the maturity of the pelage.

In areas where poultry breeding and sport hunting of forest game birds and arctic hares is developed, and also where foxes are severely infected with mange mites, the animals are killed during the course of the entire year, for instance in Estonia; from 1958, shooting of foxes was permitted year-round in the Ukraine and Georgia (which was not justified). Foxes were killed in muskrat farms also.

Organized effective shooting and trapping of foxes throughout the year using various methods (except those generally dangerous) must be permitted only in individual localities or in individual years when this species carries an obvious danger to the economy, or becomes dangerous in connection with the possibility of spreading infectious diseases. In other cases, it is necessary to promote the increase of the fox pack. Only a planned economy allows the possibility of avoiding extreme decision in respect to the species as a whole, to use it in the best manner. In Bulgaria and several countries of central Europe, the red fox is considered a useful species in agriculture and forestry. In a series of countries—Australia, Bulgaria, some states of the USA, Canada, Romania, Finland, and Yugoslavia, the taking of foxes is not limited, and in some states or estates a bounty is paid for their destruction. At the same time, according to some studies carried out in Europe and in the USA, it is acknowledged that unlimited extermination of the red fox and other predators does not confer a benefit on the protected species which serve as their natural prey, since these species begin to over-reproduce.

383 Acclimatization measures with red foxes were begun in Russia in the 17th c[entury], when the black-brown foxes were brought from Siberia to forests in the vicinity of Moscow (G. Dement'ev, 1956). In the 30's of this century, the silver-black foxes from farms were repeatedly released into different regions of the Soviet Union—Northern Territory, Lithuania and others (Parovshchikov, 1936; Ivanauskas,

1956 and others). Naturally, this benefited nothing. The transfer of the common red fox to other continents took place in the 17th and 18th c[enturies]: red foxes were sent from England to the U.S.A. Foxes brought into Australia for the control of wild rabbits acclimatized well, and resulted in its coat becoming somewhat modified. But the result of acclimatization was shown to be negative, in that the fox began to destroy not only endemic birds, but also caused great harm to populations of small kangaroo (Zhitkov, 1934, 1940; Presnall, 1958; Kastelyarnau, 1960*; Nasimovich, 1961).

The keeping of foxes in captivity was practised in previous years in the regions of the extreme North and in some districts of Siberia. Young foxes were taken from burrows and kept in primitive log coops or restrained until the time of killing. Due to the low value of skins thus obtained, this was prohibited. Commercial fur farming in the USSR has existed since 1928 and has been greatly expanded in the postwar years. American silver-black fox and forms derived from them (platinum, white-faced and snowy) are bred in captivity.

Commercial fox-raising abroad, especially in North America and in Scandinavian countries of Europe began even at the end of the past century, and by the first half of the 20th c[entury], it was very widely developed. Since the time of the Great Patriotic [2nd World] War, the breeding of foxes has considerably diminished as a result of the fall from fashion of long-haired furs, but in recent years, it is again being restored (A. Ch.).

Subfamily of Red Wolves

Subfamily Simocyoninae Zittel, 1893

Genus of Red Wolves

Genus *Cuon* Hodgson, 1838

- 1838. *Cuon*. Hodgson. Ann. Mag. Nat. Hist., I.p. 192. *Canis primaevus* Hodgs. = *C. alpinus* Pall.
- 1839. *Chrysaesus*. H. Smith. Jardine's Nat. Libr. Mamm., 25, p. 167. *Canis dukhunensis* Sykes = *C. alpinus* Pall.
- 1888. *Cyon*. Blanford. Fauna Brit. India Mamm., I.p. 142. Correction of *Cuon*.

*Not in Literature Cited—Sci. Ed.

1888. *Anurocyon*. Heude. Mem. Hist. Nat. Emp. Chin., 2. p. 102.
Anurocyon clamitans Heude = *C. lepturus* Heude = *C. alpinus*
 Pall. (V.H.).

Forms of large dimensions.

Skull heavy and massive, relatively short with broad, widely separated zygomatic arches, high (height of occipital region almost equal to half condylobasal length of skull); in adults, protuberances and crests well developed including sagittal crest.

384 Facial part of skull greatly shortened, massive, relatively wide in proximal part—distance from anterior margin of premaxilla to preorbital foramen is less than skull width at level of molars. Interorbital (frontal) region convex, this convexity (related to formation of air sinuses) extends forwards to basal half of facial part, resulting in a convexity instead of a depression on profile line at level of anterior margin of orbit. Therefore, “frontal process” is absent and whole upper profile of skull represented by quite flat convex arch. Several depressions occur only in middle part of nasal bones.

Posterior margin of nasal bone extends far behind posterior border of frontal processes of maxillary bone. (In other representatives of the family they lie at approximately the same level or the opposite relationship is observed.) Inner parts of anterior ends of nasal bones form blunt projection in middle of nasal notch. Supraorbital processes relatively small with weakly defined depression on upper surface; their ends are bent downwards. Posterior margin of toothrow extends to level of anterior margin of interpterygoid depression. Deep notch and protuberance on lower margin of lower jaw in front of angular process absent.

Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{2} = 40$. Teeth quite strong, but first

385 upper molar is weak (approximately two times smaller than in wolf), its inner blade small and carries only one cusp (in other members of the family, they are 2 to 4). On first lower molar (carnassial tooth), only one small cusp behind tall main cusp.

Canines quite massive, slightly curved and short—when jaws are closed, ends of upper [canines] do not reach or only just reach middle of mandibular bone; ends of lower [canines] reach margin of alveolus of upper [canines]. Tips of upper canines directed straight downward; the sharp cutting edge on posterior surface of canine and ribbing on lateral surfaces absent. Cutting edge of incisors without accessory lobes.

Limbs moderately long, trunk proportional, not excessively elongated; tail quite long, extending below tarsal joint, but in standing animal, does not reach ground. Pads of digits III and IV united to the rear, and form horseshoe-shaped figure open in front¹. Color uniform, quite bright, reddish.



Fig. 144. Range (reconstructed) of genus of red wolves, *Cuon* Hodgs., and species range of the red wolf, *Cuon alpinus* Pall. (V.G. Heptner).

¹This character, noted in material of Zoological Museum of Moscow University must be visible in the track (Fig. 17, p. 76).



Plate 3. Red wolves, *Cuon alpinus hesperius* Afan. et Zol., pursuing arkhar (*Ovis ammon* ssp.). Painting by A.N. Komarov.

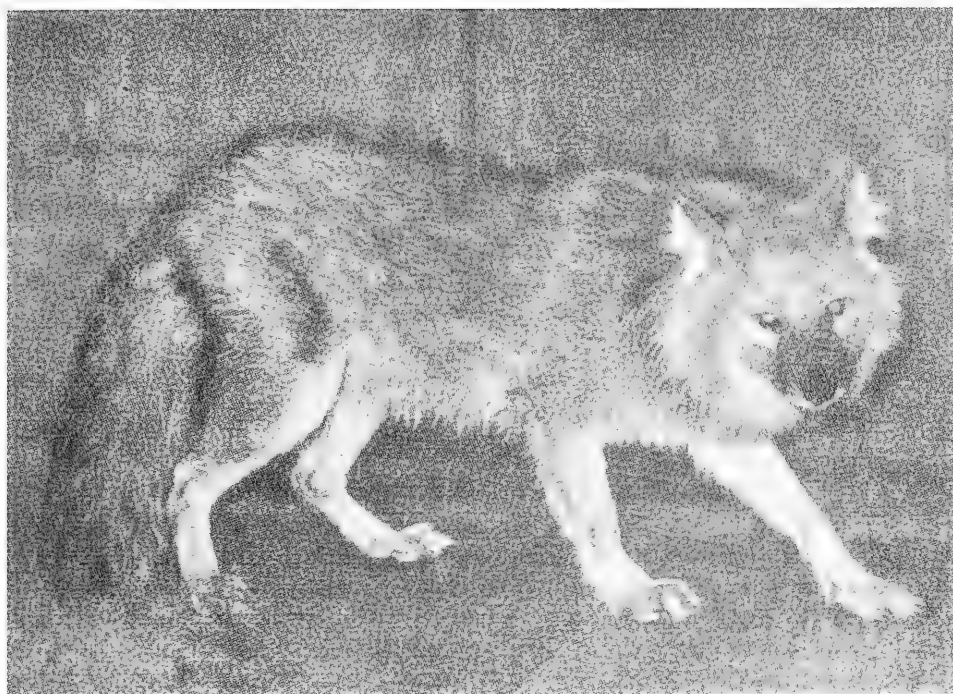


Fig. 145. Red wolf, *Cuon alpinus* Pall. in winter fur. Specimen from China in Moscow Zoo. Photograph by A.P. Zhandarmov.

There are 6 or 7 pairs of teats, occasionally 8. Sexual dimorphism is absent; seasonal dimorphism clearly demonstrated in northern forms, in southern, weakly or not manifested.

A forest, montane forest, and in part montane form. In vertical direction they attain extreme heights. Young number 2–4–7, in exceptional situations, more. Young are born in burrows, clefts in rocks, and similar places, sometimes forming even “colonial” settlements. Predators, feeding on flesh, mainly of ungulates. Even in the breeding season they remain together and hunt in packs, sometimes quite large, bringing to bay their prey.

386 The range of the genus is quite considerable and occupies the central and southern parts of East Asia. In the north, the range extends to the Amur region, Trans-Baikaliya, Altai, Tien Shan and Pamirs. In the south, it occupies Hindustan, Indochina with the Malaccas, Sumatra and Java (for more, see beyond in species description).

In its systematic characteristics, the genus is quite isolated from the other genera inhabiting the USSR, which is emphasized by placing it in its own subfamily Simocyoninae. Even if the division of the family Canidae into subfamilies is not accepted, the isolation of the genus from the above-considered assemblage must be regarded as significant. The general appearance of the animal is also characteristic (see below). It is usually accepted that the red wolves stand closest of all to the genus *Lycaon* (African hunting dogs), although the latter are markedly differentiated by dental formula (the same as in *Canis*), the color, and a series of other characters.

Reliable fossils of representatives of this genus are known from the Pleistocene of Asia and Europe. It is undoubted, however, the genus diverged and was established much earlier, and already existed in the Pliocene. There are indications of Pliocene finds in Italy. In any event, representatives of the subfamily are known in Europe from the upper Oligocene, and are near to the genus *Cuon* in the lower Pliocene. In the Pleistocene, and in part in the Holocene, red wolves were more widely distributed in the north—they lived also in the southern Urals, in the Ukraine, and westward to Czechoslovakia, Switzerland, Italy, France, Monaco and Spain, while eastward, they were found in the Holocene at Nizhne Udinsk.

The generic independence of the group is without doubt and is accepted by all investigators. The recent suggestion (Haltenorth, 1959) to unite the genus *Cuon* with the genus *Lycaon* cannot be accepted even in the very widest interpretation of the genus.

Until recent times, several species were included in the genus, but now it is accepted that it includes only one species with several races. This constitutes about 3.4% of the species in the family.

In the USSR fauna there is one species, the red wolf *Cuon alpinus* Pallas, 1811, i.e. about 0.3% of the species of mammals in the USSR.

The range of the genus in the USSR occupies the Amur-Ussuri territory, the montane southern fringe of Siberia, and the mountains of the eastern part of Middle Asia (V.H.).

RED WOLF*

Cuon alpinus Pallas, 1811

1811. *Canis alpinus* Pallas. Zoographia Rosso-Asiatica, 1, p. 34. Udskoi stockade.
1935. *Cyon alpinus hesperius*. Afanasjev et Zolotarev. Izv. Akad. nauk SSSR, otd. matem, i est. nauk., No. 3, p. 427. Aksaisk Plateau, Tien Shan.
1936. *Cuon javanicus jason*. Pocock. Proc. Zool. Soc. London, p. 51, Altai.

Diagnosis

The only species in the genus.

Description

In general appearance the red wolf is unique and is not similar to the gray wolf—in its constitution, rather, mixes features of the wolf (or jackal) and fox. It is an animal with a somewhat elongated, but proportional trunk. The tail is long, nearly half the length of the trunk, and in full winter pelage, almost reaches the ground². It is covered with very long, dense hairs which appear very thick (thicker than in the red fox).

The winter fur is dense, and quite soft and very long. The hairs on the back are especially long, where individual [hairs] reach 160 mm. On the cheeks and along the upper neck the hairs are elongated. Therefore, the head in winter fur looks small. It is wide in the zygomas, the muzzle is quite short, but pointed. Ears are large with blunt, even somewhat rounded, tips, protruding well out from the fur. Their bases are strongly approximate and they are, therefore, situated high on the head. All of this gives the animal's head a completely unique appearance, and expression which is similar neither to the red fox nor to the wolf.

*In English, also *dhole*—Sci. Ed.

²In the red wolf (in captivity) there is a completely distinctive manner—the whole appearance expresses timidity and tension, the animal seems to be flattening itself and to be slightly lame in the hind legs. With this, the end of the tail drags on the ground [see Fig. 145].

The general color tone of the whole fur is reddish, noticeably variable individually, and apparently, in part geographically (within the USSR). In the animals with brightest color in winter the back is clothed with saturated rusty red-to-reddish color, brownish highlights occur along the top of the head, neck and shoulders; throat, chest, sides, belly and upper parts of the limbs are less bright, and more yellow in tone. The lower parts of the limbs are lighter, yellowish-whitish, and on the anterior sides of the forelimbs dark brownish bands are weakly marked. The muzzle, area between the eyes, and the forehead are grayish-reddish, with color brighter on the forehead. The extraordinarily luxuriant and fluffy tail has a rusty-brownish color and is covered with brownish highlights formed by the dark tips of the guard hairs. At the end, this highlight is denser and the tail darker. The underfur and the bases of the hairs are in color gray of various intensities, sometimes with a more or less marked touch of yellowish.

Paler and duller colored individuals have a tone from ochereous reddish to grayish-rusty. Chin, throat, bottom and sides of neck, belly and the lower parts of the sides are white with a more or less developed ochereous or light ochereous highlight. The tail is reddish-ochereous in its main part, darker due to the brown tips of the hairs in its distal half and especially at its tip; below it is lighter. In particularly light-colored individuals, darkening of the tail is almost undeveloped.

In some individuals, the general color is dull with weakly developed rusty-red tone.

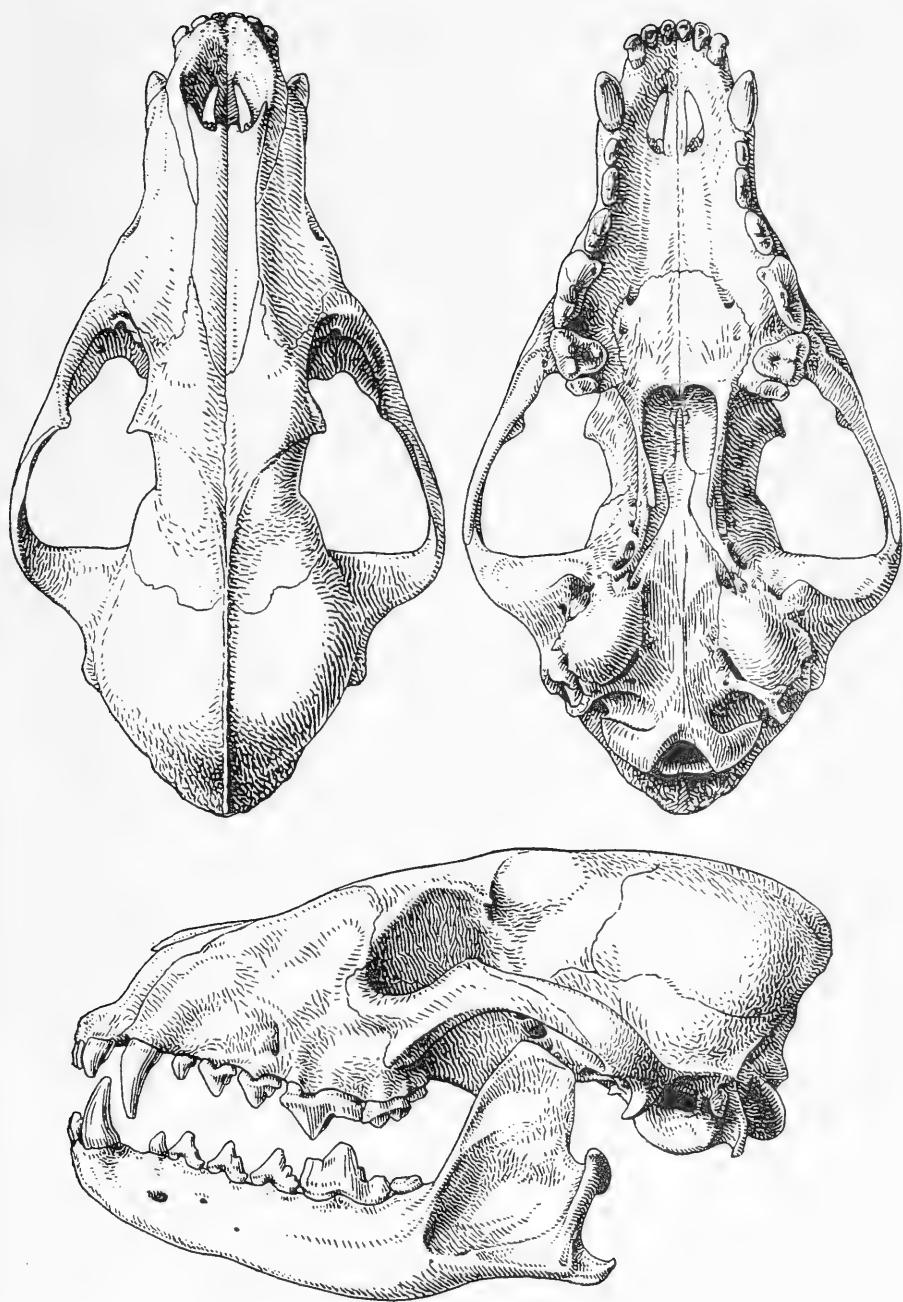
Summer fur coat is much shorter than the winter, coarse and darker, brownish. The tail, however, is covered with fluffy long hairs.

For characteristics of the skull, see description of the genus.

Body length is 103 cm, tail length 48 cm. Hind foot length 22 cm, ear length 8 cm³.

Greatest length of skull 171.0–200.0 mm; condylobasal length of skull 174–188 mm; zygomatic width 103–118 mm; width of cranium 61.0–68.3 mm; skull height in region of tympanic bullae 70–73 mm, length of muzzle from orbit to the alveolous of incisor 70.0–81.5 mm;

³Measurements of one specimen from Ussuri territory (Ognev, 1931). For red wolf from the Himalayas *C. a. primaevus*, body length is given as 92–96 cm and weight, 17.3 kg (Pocock, 1941).



length of nasal bone 53.2–71.5 mm; length of upper tooth row 74.0–80 mm.⁴

In connection with the rarity of the red wolf in the great part of its range in the USSR, the number of skins and skulls in our museums is very few. Therefore, it is impossible to give a sufficiently full picture of variation in this species in our country (V.H.).

389

Systematic Position

Only species in the genus.

Geographic Distribution

South, Central, and southern half of East Asia.

Geographic Range in the Soviet Union

This represents the narrow northern margin of the range and occupies a negligible part of the country—the southern fringe of the Far East, eastern and middle Siberia, and the eastern part of Middle Asia.

In the east, the northern border of the range of the red wolf begins at the shore of the Pacific Ocean in the region of the lower Uda (Udskoi stockade).

In spite of the assertions of some earlier authors (Shrenk, 1858; A. Nikol'skii, 1889) perpetuated also in recent literature (Ognev, 1935; Ellerman and Morrison-Scott, 1951), the red wolf is not and never was on Sakhalin. From Uda, the range boundary goes westwards somewhat to the south of the Stanovoi range and passes a bit to the north of the northern bend of the Amur, not reaching the main axis of the Stanovoi range here (in Gilyui and Ol'doi, this species is not recorded⁵). This is the most northerly habitat of the red

⁴Figures according to somewhat contradictory data in literature (Ognev, 1931; Afanas'ev and Zolotarev, 1935; Novikov, 1956) and they may give only a general representation of skull dimensions.

⁵Information concerning the penetration of the red wolf into the Stanovoi mountain range given from old authors (Maak, 1861; Radde, 1862) is somewhat contradictory. Apparently, it should be understood thusly: to the west of the range in the region of the northern bend of the Amur, the animal penetrated nearer to the main axis of the range than in the east, where it apparently did not spread farther than the foothills (according to Radde, it was also rare in the Bureinsk mountains). It must be taken into consideration that the known contradictions of the proposed text with the texts of the referenced authors and that of Ognev (1935) are explained not only by some new data and corrections, but also terminology—not too long ago, the Stanovoi range was frequently called Yablonovoi. This appears as an error of some contemporary authors.

wolf in our country and the most northern part of the range of the species.

Extending farther, to the north of southeastern Trans-Baikaliya and the upper Onon, the range boundary goes westward somewhat to the south of the southern end of [Lake] Baikal (it was recorded in particular at the source of the Dzhida) and covers the Eastern Sayan (sources of the Irkut and Oka).⁶ Farther, the range enters Tuva (known from Tanna-Ola) and, apparently, that more easterly part of the Western Sayan which lies in the region of Us' basin and northwest of the city of Kizyl (Turan and Kurtushibinsk range—former Usinsk region).

In Altai, the range occupies only the southern part of the country—Chuisk steppe and the region along the Chuya river, the area of the upper Argut (Dzhassater-Yassater), and northwards to Uimon at the source of the Katun [river]. To the west, the range enters the upper Bukhtarma (Belaya Berel') and the region of Lake Markakol'. Farther, the boundary, enclosing the Tarbagatai and Saur, exits into China.

The boundary again enters our territory as a small extension, which includes the Dzhungarsk Alatau and again exits into China, entering our country once more along the Zailiisk Alatau. Further on, it covers the whole Tien Shan including Kirgizsk (Aleksandrovsk) range, Chatkal'sk and Talassk ranges and the ranges bordering the Fergana valley on the north; the Alai system and Pamirs. Usually, its occurrence is only documented for the East Pamir. This species probably exists also in the West Pamirs; however, information concerning the Pamirs, as in general about all the mountains of Middle Asia, is extremely rare. Apparently, the animal is absent in the Turkestansk and Zeravshan ranges, as well as in the Gissar. From Pamir, the boundary passes into Afghanistan (Kafiristan) and Kashmir.

391 The defined line of the northern limit of the range of the red wolf is ill-determined. In many places, the animals are either extremely

⁶In the eighteenth century, it was recorded considerably further north—in the upper Lena (Pallas, 1811—"e superiore regione Lenae fl. albatius, vidi"). These statements of this almost impeccable author are hardly simple errors (it is characteristic that Pallas constructs the phrase in the plural). Probably, at that time, the animals were distributed, perhaps transient, considerably more to the north than in our time or even in the nineteenth century. In early times, in such places mountain sheep (*Ovis canadensis**—see vol. I), apparently existed.

*Now usually referred to *O. nivicola*—Sci. Ed.

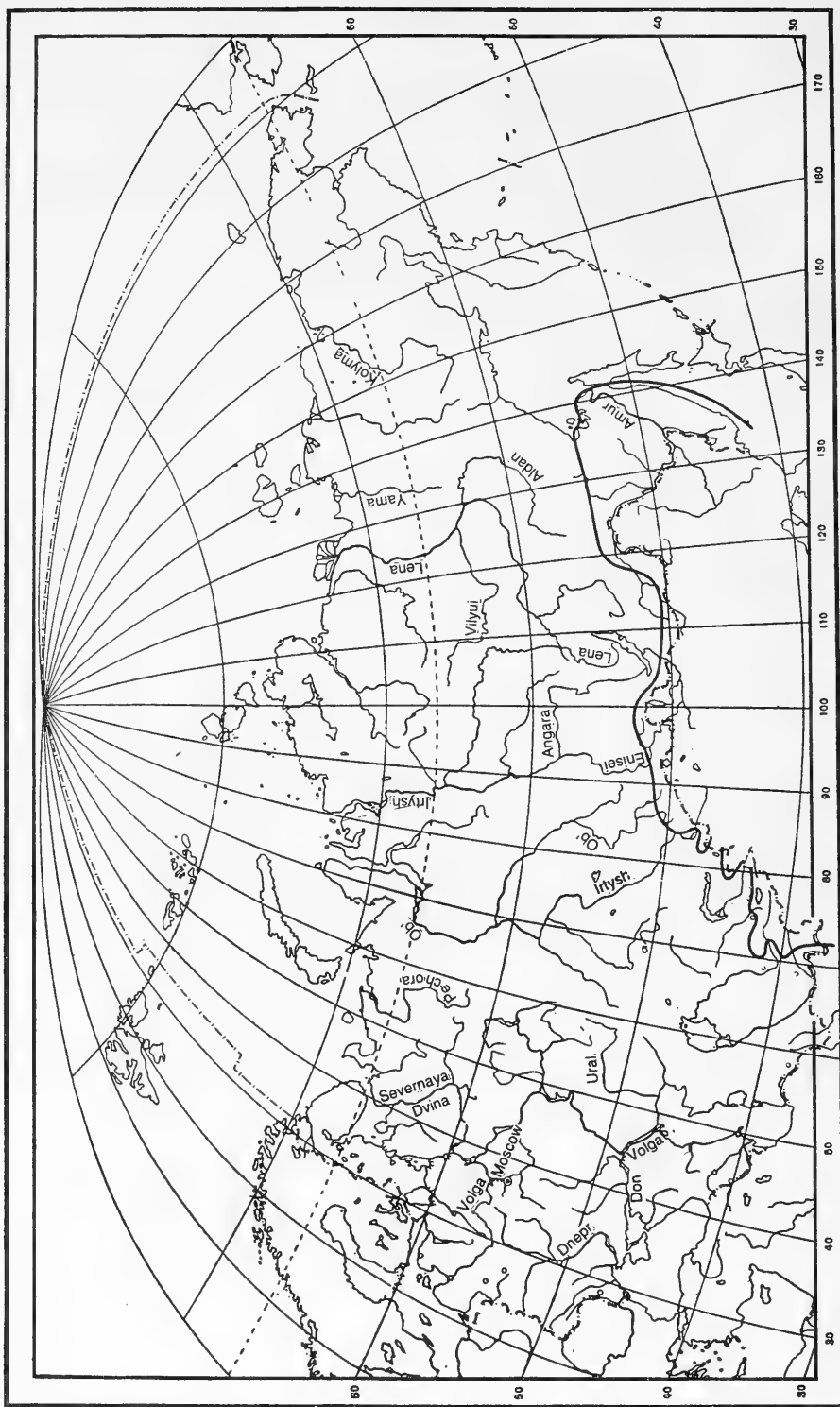


Fig. 147. Limits of distribution of the red wolf, *Cuon alpinus* Pall., in the USSR. Reconstructed range (V.G. Hepner).

rare or they appear fortuitously at intervals of several, or even many years. With respect to some areas, there are only old reports, unconfirmed in recent times. Lastly, information about some territories, especially those such as Trans-Baikaliya are often contradictory. The picture described here, discounting chance circumstances, is explained not only by natural instability at the [range] limits but also populations at the edge of the range. Long-distance movements and displacements, at least in some parts of the range are a characteristic tendency for the red wolf (see below).

The red wolf is more common, and more or less regularly encountered, in the Ussuri territory, mainly in its southern part; rarer, but also appearing more often than in other places (except southern Ussuri territory), in the Tien Shan. Judging by data from old authors, populations of red wolf within our borders considerably decreased during the last 100–200 years. Apparently, the range has also contracted, in any event the area more or less permanently inhabited.⁷

Geographic Range outside the Soviet Union

This extends from the northern limit as defined, southward through the whole of Central and South Asia including Indochina and Malacca, Sumatra and Java and the whole of Hindustan, except its northwestern desert sections and the extreme south. Here, the range extends to Kurg (about 15° N. Lat.) and the Nilgiri Hills (11° N. Lat.). Absent on the Japanese islands, Taiwan, Hainan, Borneo and Ceylon. Information concerning its occurrence on Borneo, repeated in recent literature, is undoubtedly mistaken. The red wolf is, apparently, absent in Iran also. Several suggestions (Byalynitskii-Birulya, 1912; Ognev, 1931), based on data about Iranian Baluchistan (Zarudnii, 1931), were not justified.

Within the outlined range, the red wolf has in places been exterminated or crowded out by humans (East China and some parts of India), and in other places it disappeared over significant expanses without human interference. Such places include, apparently, some parts of Tibet (in the Himalayas, around Lhasa in northeastern Tibet,

⁷Range according to data of Pallas, 1811; Radde, 1862; N. Severtsov, 1873; Kashchenko, 1900; Bikhner [Büchner], 1902; Polyakov, 1914; Zarudnyi, 1915; Tugarinov, 1916; Gassovskii, 1927; Kashkarov, 1927; Ognev, 1931, 1940; Yanushevich, 1952; Kuznetsov, 1948, 1948a; Sludskii, 1953, 1939; Shnitnikov, 1936; Spangenberg, 1936 and other authors.

in the Nan Shan; it is present in northern Kashmir—Ladak, Gilgit and Chitral), desert and steppe areas of Inner Mongolia (present in montane sections of Dzhungaria and Kashgaria), some (steppe) parts of northeastern China, eastern and central parts of the Mongolian Republic etc. Generally, the species is characterized by its peculiar movement—irregular migrations—and also translocations within the range. In some places in the center, and not only on the northern edge, of the range, individual populations may move into other territories where they had long been absent and then abandoned their territory after several years. This is possibly connected with the extermination of the large game by the wolves themselves (V.H.).

Geographic Variation

Geographic variation of the red wolf is, apparently, well manifested. Usually, 11 subspecies are recognized (Pocock, 1936; 1941; Ellerman and Morrison-Scott, 1951), which is, undoubtedly, exaggerated. In our country, 2 subspecies may be accepted (Afanas'ev and Zolotarev, 1935). They are real, but their characteristics, due to collection materials scarcity, cannot be considered well established.

1. Ussuri red wolf, *C. a. alpinus* Pallas, 1811.

General color tone of winter fur is intense rusty-red. Head dorsally, and outer side of ear, brownish-rusty; whole dorsal surface of neck is same color, with blackish-brown highlights, shoulder and entire upper surface of back brownish-rusty with black-brown highlights, outer side of legs rusty-brown color, lower side of body and inner side of legs with noticeable yellowish tint.

Facial part of skull relatively narrow, forehead convex, nasal bones elongated.

Dimensions comparatively large—greatest length of skull 180–200, averaging 189 mm; length of nasal bones averages 66 mm.

Eastern part of the range in our country—from Pacific Ocean to East Sayan. Western limits are not accurately known, but the Altai is apparently not included in the range.

Outside the USSR, in the Mongolian Republic, northeast China, and from eastern China southward, apparently, to Gansu, Sichuan and Kam. Southern and western limits of distribution are not precisely known.

Well differentiated, apparently the largest form, intense coloration.

2. Tien Shan red wolf. *C. a. hesperius* Afanasjev et Zolotarev, 1935 (synonym *jason*).

General color tone of winter fur lighter, with weakly developed rusty-red tints. Head dorsally, and outer side of ears reddish-straw color, dorsal surface of neck dirty-white; along dorsal surface from ears to shoulders runs narrow band of sandy-yellow color, shoulders and entire upper surface of back faded yellow-brown color, outer surface of limbs light sandy-yellow, ventral side of body and inner side of limbs have no, or weakly developed, yellowish tint.

Facial part of skull relatively wide, forehead weakly convex, and nasal bones shortened.

Dimensions relatively small—greatest length of skull 171.0 to 194.0, averaging about 180 mm; length of nasal bones averages about 57 mm.

Western part of range in USSR—Altai, Tien Shan and, apparently, Pamir.

Outside the USSR, the range of this form is unclear. Apparently, it is distributed in China—along the Tien Shan and along the system of ranges of the Kun Lun to Kukulun (Afanas'ev and Zolotarev, 1935). It is possible that its range is wider, and occupies the southwestern part of the [species] range (Kashmir, see below).

A form, well-differentiated from the nominal, but, apparently, very close, if not identical with, that occupying Kashmir and West Tibet.

Beyond the borders of the USSR, the following forms are usually recognized (Pocock, 1936; Ellerman and Morrison-Scott, 1951, and others):

1) *C. a. dukhunensis* Sykes, 1931—India south of the Ganges; 2) *C. a. primaevus* Hodgson, 1833—Kumaon, Nepal, Sikkim, Bhutan; 3) *C. a. lepturus* Heude, 1892—China south of Yangtze-Kiang; 4) *C. a. infuscus* Pocock, 1936—Tenasserim; 5) *C. a. fumosus* Pocock, 1936—western Sichuan; 6) *C. a. laniger* Pocock, 1936—Kashmir and southern Tibet to Lhasa; 7) *C. a. adustus* Pocock, 1941—Upper Burma, Indochina; 8) *C. a. sumatrensis* Hardwicke—Sumatra; 9) *C. a. javanicus* Desm., 1920—Java.

It is quite evident that some of these forms are unfounded, for example, those described from the southeastern part of the species range. Probably, within the species limits, are not more than 4–5, and not 11, forms.

In geographic variation of the species, Bergman's rule is, apparently, manifested quite well—compared to large animals from the northeastern part of the range (nominal form), animals from the south-eastern are noticeably smaller (V.H.).

Biology

Population. Extremely rare in the West Pamir, in Alai and western Tien Shan (in Fergansk and Chatkal'sk ranges, Talassk Alatau, Susamyrtau, Kirgizsk range), the northern (Zailiisk Alatau, Kungei 393 Alatau) and central Tien Shan (Atbash' range, Tersk Alatau and others), where it is caught individually, and not each year. In the 30's of the present century, in Kirgizia, 1 to 3 skins were tanned and also not each year (Shnitnikov, 1936). From 1922 to 1956, a total of only 6 skins were tanned there (D. Dement'ev et al., 1956). Somewhat more often, it is met with in the Dzhungarsk Alatau and its eastern spurs, the Tarbagatai and Saur. In Tarbagatai, at the beginning of the 20th century, it was common (Plotnikov, 1912). In Saur and in the eastern spurs of the Dzhungarsk Alatau, for instance, in the Alakul'sk region, up to 6 red wolves were captured in a season in various years (Khakhlov, 1928; A.A. Sludskii).

It is extremely rare in southern Altai (Kashchenko, 1899; Polyakov, 1914; Berger, 1946; Nasimovich, 1949). In the middle of the last century in the Altai, it seems it was encountered somewhat more often. In the ranges of the West and East Tannu-Ola and East Sayan, it is rare (Radde, 1862; Solov'ev, 1921; Shukhov, 1925; Podarevskii, 1936; Yanushevich, 1952). In the Sayan and Okinsk territory and Tafalaria, where in past years it was still sometimes found in packs of 5–10 individuals, only a few are obtained individually and not every year.

The red wolf is rare in the mountains of the southern part of Pri-Baikal (Dzhidinsk and other ranges), in Trans-Baikaliya in the ranges lying in the upper Onon river, on the northern slopes of the Great Khingan and in the southern slope of the Stanovoi range, as well as in the Dzhagda and Bureinsk ranges, although earlier it was common in this region, and in some places, abundant (Maak, 1861; Radde, 1862). It is more often encountered in the Little Khingan and in its foothills, and in the southern half of Sikhote-Alin. Earlier, it was relatively common in the southern Ussuri territory, on the Yankovsk Peninsula, and on the Iman (Ognev, 1931).

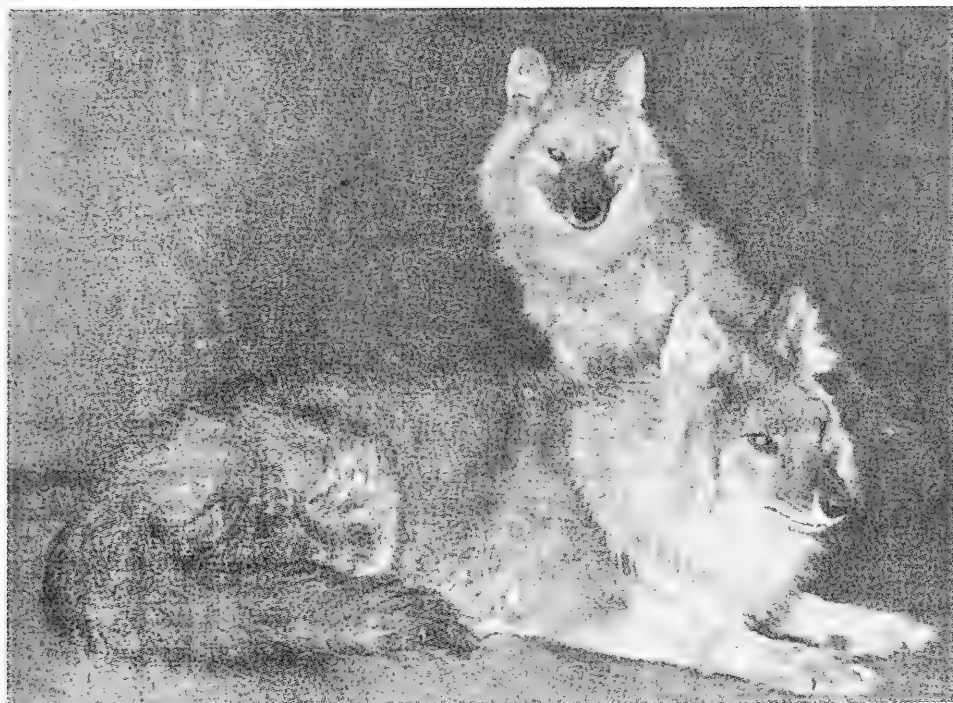


Fig. 148. Red wolves in winter. Specimens from China in the Moscow Zoo.
Photograph by A.P. Zhandarmov.

Habitat. In Middle Asia and Kazakhstan, the red wolf is met with in summer in the alpine and subalpine belts at height of 2,500–4,000 m above sea level. Here, it occupies rocky heads of ravines, where
394 there are many Siberian ibex, or on the high-lying plateau—*syrt*, on which arkhar sheep are common. With the formation of deep snow cover in the mountains, the red wolf follows after the ungulates, moving to sunny southern slopes and to other light-snow regions. At that time, it descends to the zone of spruce or juniper. In the lower zones of the mountains, the wolves remain until the beginning of summer, where at that time the females and lambs of the ibex, arkhar sheep and roe deer dwell. In the spurs of the Dzhungarsk Alatau and in the Tarbagatai, the red wolf was observed on gradual slopes interrupted by rocky gorges, at a height of only 800–1500 m above sea level. At such height here, ibexes, arkhar sheep and roes live.

In Altai, Sayan, Tannu-Ola and in Pri-Baikal, this animal is found in summer in balds and high montane valleys with steppe vegetation, ascending to a height of 1,500 to 2,000 m (Solov'ev, 1921; Yanushkevich, 1952; A.A. Sludskii), but with the formation of the deep snow cover, it departs to light-snow sections. In the mountains of eastern Siberia, it was observed both in balds, and in taiga having rock outcrops, along the lengths of rivers and badlands. It is attracted to such places by the abundance of ungulates and the shallow, compact snow cover. In the Far East, the red wolf lives not only in the low mountains and foothills covered with Okhotsk taiga, or forests of the Manchurian type with mixed deciduous species, but sometimes descends to the seacoast.

Therefore, within the boundaries of the Soviet Union, the red wolf is, in the greatest part of its range, a typical montane animal, being that in the western half it lives, for the major part of the year, high above sea level in alpine meadows and high-montane steppes. In the eastern part of the range, this same carnivore is mainly an inhabitant of montane taiga, although here it ascends to balds; occasionally it even appears along the seacoast. Everywhere it is restricted to rocky places, in which it can take cover in case of danger.

The red wolf has a fluffy, dense fur with well-developed underfur, and its tail is also exceptionally fluffy. The ear tips are rounded and are covered internally with dense wool. All these characteristics testify to the adaptations of this animal as an inhabitant of severe conditions.

Sometimes, red wolves appear in lands not familiar with them. Thus, in 1901, on the Irtysh river, 70 km south of the city of Pavlodar and about 150 km from the nearest mountains (Bayan-Aul), 2 red wolves were caught on the grassy steppe. Earlier, these carnivores were also observed there (Plotnikov, 1901, 1912). In the winter of 1954/55, a pair of red wolves appeared in the region of Smidovich (west of Khabarovsk) in typical forest-steppe. Apparently, the animals moved to the forest-steppe from the Bureinsk range, avoiding the deep snow cover (Sysoev, 1955, 1960).

In the Mongolian Republic, it lives in balds and foothill steppes. On transiting from one group of mountains to another, it crosses great expanses of dry steppes and deserts. It was observed on the strongly desertified Tsagan-Bogdo range, which is rich in cliffs (Bannikov, 1954). In India, Burma, on the Indochinese peninsula, in Indonesia and China, the red wolf inhabits the mountains from the alpine zone

(Himalaya and Tibet) to the foothills; preferring forest regions. In the south of the range, it is common also on the plains and frequently encountered on the seashore.

Food. Information about the food of the red wolf within the Soviet Union is almost lacking. In the mountains of the Tien Shan, and in the Tarbagatai and Saur, red wolves hunt Siberian ibex, arkhar sheep, roe deer, maral [wapiti] and wild swine. The most frequent prey of this predator is the ibex. It very rarely attacks domestic sheep. In the Altai and Sayan, the list of animals that the red wolf hunts is expanded to musk deer and reindeer. In eastern Siberia, the red wolf preys, apparently, on roe deer, Manchurian wapiti, wild swine, musk deer, reindeer, and in Primor'e, on spotted [sika] deer and goral as well. Wolves appearing on the Yankovsk peninsula systematically attacked spotted deer located in deer farms, and roe deer (Ognev, 1931).

In summer in the central Tien Shan, wolves made use, in their diet, of plant in large amounts, mainly mountain rhubarb [*Rheum*]. This plant was always found in dens with pups, as if the wolves fed it to the young, regurgitating the half-digested closed blossoms of the rhubarb. The hunters, capturing live red wolves, fed these blossom to the young captive animals (Shnitnikov, 1936).

In the Mongolian Republic, red wolves mainly hunt argali sheep, more rarely, Siberian ibex (Bannikov, 1954). In China and India, red wolves attack deer, sambars and muntjacs; antelope, mountain sheep, wild swine, and even large wild oxen—banteng and gaur, as well as domestic buffalo, horse and pigs. Packs of red wolves possibly dare to attack bears, leopards and even tigers, sometimes driving them away from their prey (Jerdon, 1874; Tate, 1947; Shaw, 1958 and others).

Home range. Not established.

Burrows and shelters. No accurate data exist for the USSR. It is known that for temporary lairs and whelping, they occupy small natural caves, abandoned burrows of other animals, but rarely dig their own. It has been suggested that sometimes several females whelp in one den (India; Jerdon, 1874).

Daily activity and behavior. Red wolves hunt at any time of day or night, but more often during the daytime. In the Tien Shan mountains, they were repeatedly observed pursuing prey during the day. The red wolf runs more slowly than the jackal and red fox, but has great endurance and can chase its victim for many hours. It is cautious and,

therefore, not easy to observe or hunt, but in attacking its prey, especially when very hungry, it is daring and often kills its victim in front of humans.

Except during the breeding period, the red wolf lives and hunts in packs. In a pack occur 5 to 30, and sometimes more animals, but usually 5–10. Thus, a pack of 5 animals was observed in late autumn, 1937, in the Kirgizsk range (Shnitnikov, 1936; D. Dement'ev et al., 1956). In the Sayan, packs of 5–12 individuals were observed (Solov'ev 1921; A.A. Sludskii). In spring, in Primor'e, a pack of 6 was noted and in winter up to 20 wolves (Ognev, 1931). This animal hunts in China and India in packs of 5–10 individuals, rarely more (up to 30) (Jerdon, 1874; Baikov, 1915; Tate, 1947; Shaw, 1958; A.A. Sludskii; according to observations outside the borders of our country).

Upon marking prey, the carnivore follows it for a long time, driving it until able to get close to it. On running down a large prey, they seize it by the thigh or side in the region of the groin, inflicting wounds until the pursued animal falls. After bringing down a large animal, the wolves sometimes bite its throat. Sometimes several wolves run after the prey, while others run across to intercept. Cases are known when red wolves drove the pursued animal to a precipice where they killed it (Radde, 1862; Jerdon, 1874; Bourlière, 1955).

According to G. Radde (1862), wolves upon sighting prey, utter special whistling and hissing sounds, but this report needs new confirmation. Based on observations made in India, when pursuing prey, they give a peculiar yelp from time to time, or else chase it in silence.

The idea that for a human to encounter a pack of red wolves may be very dangerous (Radde, 1862; Sowerby, 1923) is a clear exaggeration. In the Tien Shan, cases of attacks on humans are unknown. In India, where this predator is common, attacks by it on humans are also unrecorded (Ryabchikov, 1950); rarely, it attacks domestic animals there.

396 *Seasonal migrations and transgressions.* The sudden appearance of a pack of red wolves at first one, and then another, place, and then their disappearance for a long time, provides the foundation for suggesting that, apart from the breeding period, they roam widely in search of prey. With the appearance of their packs in a region rich in ungulates, the carnivores systematically hunt, quickly dispersing them, after which they are obliged to search for new hunting areas. In the Tien Shan, red wolves do not live permanently in one place, and they sometimes appear in those regions where they were previ-

ously not known, live there for some time and then disappear, but after an indeterminate period of time they reappear. In the Chatkal range, wolves always appear from the east, i.e. from the main montane node of the Tien Shan (Shnitnikov, 1936). In Kazakhstan, cases are known when red wolves appeared in the Chingiztau range (Karelin, 1841), whence they would pass from Tarbagatai, crossing in a straight line for about 180 km. In order to reach Yamyshyevskii village on the Irtysh river (see above), they must have traveled in a straight line about 600 km from the Tarbagatai. The wolves which appeared in the former Smidovichesk region must have covered about 180 km, traveling from the Bureinsk range.

Up to now in the Soviet Union, dens of the red wolf with young were found only in the central Tien Shan. It is possible that they generally do not reproduce at all in many regions within our country, and that, of the red wolves which appear in the mountains of our country, the majority only temporarily migrate to us. In the Mongolian Republic, the appearance and disappearance of red wolves in isolated free-standing ranges testify to their wide wanderings in this country, during which they cross hundreds of kilometers through dry steppes and deserts.

Reproduction. In the USSR, reproduction of the red wolf is unstudied. According to observations in the Peking [Beijing] Zoo, its rut occurs in January–February, and whelping in April. The period of pregnancy is 60 days. In the course of a year it bears one litter. In a litter of wolves in Peking Zoo, there were usually about 5 pups and up to 9 (Krumbigel, 1954; Shaw, 1958). Apparently, larger litters may occur, since the female has from 12 to 14 teats. The newborn pup has a dark brown color.

Growth, development and molt. Not studied.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Enemies include gray wolf, tiger, leopard and snow leopard. These carnivores, at the same time, are manifested as competitors. Diseases and parasites are unstudied. Population dynamics are not clear. It is only known that, sometimes, red wolves become more common in one or another place, a fact which is, however, associated with their migrations from other regions (see above).

Field characteristics. Dimensions as in the juvenile gray wolf in October, but with shorter limbs. The tail is longer with a fluffy end which reaches the ground; in winter, covered with long wool, similar to the fox. The animal does not lift the tail above a horizontal line. Thanks to the ochreous-reddish-ginger color of the fur, the carnivore

is touted as “beautiful”* from a distance, while the gray wolf, some distance from the observer, looks almost white. The voice resembles the yelp of a frightened dog and is not similar to a bark. The red wolf, in contrast to the gray, does not howl (D. Dement'ev et al., 1956) (A.S.).

Practical Significance

A fur-bearer, but because of its small number, it has no value in fur tanning of the Soviet Union. It is not present in the fur standards and its skin is accepted as that of gray wolf under the name “half wolf”. Sometimes, skins of this animal are accepted as dog.

The winter skin of the red wolf with its long dense fur was highly valued in the past by the Chinese, and the end of the 60's of the previous century in the Ussuri territory, they cost 3–4 silver rubles (Przheval'skii, 1870), while at the beginning of the current century in 397 Manchuria, its price reached 8 rubles (Baikov, 1915). At the present time the price of a prepared skin of the red wolf is from 1 to 4 rubles. In Semirech'e, *dokha* [fur-coats] from the skins of the red wolf are considered the warmest and are very costly.

Because of its small numbers and its cautiousness, it does not harm livestock, although red wolves infrequently attack spotted deer kept in parks (Menard, 1930; Ognev, 1931).

P.S. Pallas (1811) who first described the red wolf, put forth the suggestion that this carnivore participated in the formation of some domestic dog breeds; this idea is lacking in any foundation.

Taking into consideration that the red wolf is extremely rare, and thanks to its small numbers causes no harm to the hunting economy and livestock breeding, its special pursuit is not desirable. Until now, hunting has been permitted throughout the year, and in Kirgiziya, a bounty of 50 rubles is paid for each animal taken (A.S.).

Family of Bears

Family URSIDAE Gray, 1825

Carnivores of a generalized type, of large and very large size (this family comprises the largest species of the order); they are heavy and clumsy in built.

* The Russian phrase “*Krasnye zver*” means “fine animal”—Sci. Ed.

Plantigrade, with broad, massive and short hands and feet. While moving (at least our bears), they usually rest not on the whole front limb but only on the anterior part of the fore limb only (digits and anterior part of the metacarpal region). When moving faster, the animals also do not rest on the entire hind limb (this is easily seen in their tracks). In this way, they are, to a certain extent, digitigrade animals. The bear rest upon the whole surface of the foot only when moving very slowly or while standing.

Five digits, on anterior and posterior limbs of almost similar length; all digits touch the ground. Their pads form only a slightly curved line—pads of fingers II, III and IV lie only very slightly anterior to the line on which are found pads I and V. Claws not retractile, very long, curved in a sickle-shape and compressed laterally; on anterior limbs they are significantly, sometimes twice, as long as on posterior limbs.

On lower surface of fore- and hind-foot, on anterior part of feet themselves, except for digital pads there are transverse naked areas (plantar and palmar callosities), and also bare areas behind them. In different species, their relative size and form are very different; on hind foot, they are usually larger. In some cases, entire lower surface of fore- and hind-foot entirely covered by a large callosity. Last phalanges of digits not capable of much upward flexing and have normal articular surfaces.

Skull relatively large and massive, in majority elongated; facial part elongated and strong, with relatively long jaws, or else jaw and facial part are much shortened (Malayan [sun] bear, *Helarctos*). Zygomatic arches strong, fairly broad and general skull outlines proportional, or facial part very short and zygomatic arches very widely divergent laterally (Malayan [sun] bear). Contours of skull sharp, sagittal (main posterior part) and occipital crests usually well developed; at point of their divergence, a posterior projection is formed. Line of upper profile more or less convex, its highest point usually located somewhat behind supraorbital processes.

398 Profile of facial part of skull concave in posterior section. Orbit relatively small, temporal fossa very large. Mastoid region wide, and forms behind posterior base of zygomatic arch a well-defined laterally directed process in forms of a platform. Paroccipital process well developed, located quite far from tympanic bulla. Osseous tympanic bulla usually flattened, partition in internal cavity absent; auditory meatus in form of elongated tube. Alisphenoid canal present. Bony

palate narrow and elongated, its posterior edge lying behind posterior point of last molar. Posteriorly, posterior palatine foramen relatively far posterior, and located at level of last molar. On lower jaw, below angular process, is a small inwardly directed alveolar process.

Complete dental formula (typical) is $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42$, in one

case, $I \frac{2}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 40$, (middle incisors absent [sloth bear]) and

in another, equivalent to normal, very commonly $P \frac{3}{3}$ and $P \frac{2}{2}$ (reduc-

tion of second and third premolars in association with extreme shortening of facial part), i.e., total of 38 and 34 (*Helarctos*). Even in forms with complete dental systems (*Ursus* s.l.), as individual and age-related characteristics, there is loss of some of the anterior three premolars, especially the second upper and second and third lower. Frequently, therefore, even in species with complete dental formulae

(brown bear), it may take the form: $I \frac{3}{3} C \frac{1}{1} P \frac{2}{2} M \frac{2}{3} = 34$. Incisors form

a weakly convex line, lateral larger than [two] interior, sometimes considerably; canines strong, broad at base. Entire cheek tooth row and canines form almost straight line, hence both rows parallel, first three premolars in both jaws small, conical, have only one root and frequently absent (fallen out).

True carnassial teeth do not develop. Fourth upper premolar small (smaller than first molar), usually having three blunt cusps—one anterior and two posterior. It is remarkable that it has two roots and is situated anterior to the infraorbital foramen and is the point of maximum mechanical force. Upper molars large, with broad low crowns without cutting elements on surface. First has four more or less clearly defined cusps, separated by a middle longitudinal fissure. Second upper molar larger than first, extending in longitudinal direction, with large "heel" and a broad longitudinal groove in middle; two cusps are located on its outer side.

In lower jaw, fourth premolar small, conical in form; first molar elongated, with three cusps on outer part and well developed heel, usually carrying two cusps. Second molar more or less same length as first, but broader. In middle, has longitudinal fissure, outlined by

marginal crests, in which are elements of two cusps. Third molar smaller than others, with flat, slightly projecting cusplets, outlined by low rim.

Præputial orifice situated far anterior to scrotum. Penis long, *glans penis* smooth, without spines. *Os penis* present. Size of bone quite large, tapered on end, longitudinal groove absent. Anal glands absent or extremely poorly developed. Tail very short, usually hidden in fur and unnoticeable. Ears rounded, upright, in some species quite large, in others hardly protruding from fur. Eyes small. End of nose bare and lips, both upper and lower, large and movable.

399 Pelage long and shaggy, in northern and montane forms, thick; except in one species (*Helarctos*), short and quite sparse. Color monotone—white, black or brown of various tones—from golden or yellow-brown to dark brown. Individual and geographic variation in color very great in some forms (brown bear, *Ursus arctos*); in majority of forms, color is stable. In one species (American black bear, *Ursus americanus*), color is triphasic—black, brownish, and “blue”.*

In some species, qualifying as a constant character is a white spot on the chest (white-chested or Himalayan black bear, *Ursus tibetanus***, Malayan sun bear, *Helarctos*), or it appears in the nature of individual deviation (brown bear; American black bear *Ursus americanus*), sometimes developing as a light collar; in some forms, a particular color of muzzle qualifies as a permanent character (light, brownish—American black bear, Malayan bear), or a light ring around the eyes (spectacled bear, *Tremarctos*), etc.

One pair of pectoral teats. In several species (brown bear), there are three pairs, but only one pair of functional mammary glands. It is possible that this also occurs in other species, but data on this are lacking.

Sexual dimorphism in color and other characters is absent, but males are larger than females. Age morphism, as a rule, is also absent, or is weak (young brown bear although monotone, usually has a light spot on chest or neck). Seasonal dimorphism is considerable only in northern forms and is expressed in different length and thickness of winter and summer fur. There is only one molt annually.

In general appearance, all species of the family are quite homogeneous, and represent insignificant deviations from one bear type.

*A whitish phase is also known—Sci. Ed.

***Sic*; should be *tibetanus*—Sci. Ed.

All have a weighty general structure, which is emphasized by absence of tail, and in the majority, long shaggy fur; legs are short with large, sometimes with extraordinarily long curved claws; head is large, heavy, usually furry, with small, deeply set eyes, withers in the majority are high. Depending on development of climbing ability, whether they are more or less arboreal, or, on the contrary, purely terrestrial in way of life, the degree of massiveness of anterior and posterior parts of the body differs. In a purely terrestrial form (polar bear), the posterior part of the body and muscles of the hind legs are especially developed; and in a good climber (white-chested bear, sloth bear, Malayan bear), anterior part of the body and muscles of anterior extremities are especially developed.

Differences in size of different species are slight. The largest species (polar bear, brown bear) in their largest forms have a maximum body length of 230 to 300 cm; a height of 135 cm at the shoulder, and a weight of 500 to 700, and even, apparently, 1000 kg (brown and polar bears). The smallest species (Malayan bear, *Helarctos*) has a body length averaging 115 cm and a weight of 50 to 100 kg (Pocock, 1941). Therefore, the ratio between the weight of extreme forms constitutes 1 : 10 or less.

Bears are mainly associated with forests of the plains and mountains of temperate latitudes and tropics, and often in forestless montane regions; only one species inhabits the shores of the Arctic Ocean and on arctic ice, being a semiaquatic animal. In a vertical direction, its distribution is from sea level to alpine meadows and the highest plateaus of Central Asia.

The bear usually moves slowly with heavy steps; in case of danger some run very rapidly; some species swim well. All except the polar bear climb trees well (brown bear only when young); some represent quite highly developed specialized arboreal forms (sloth bear, *Melursus*; Malayan bear, *Helarctos*), with some particular adaptations (structure of the fore-limbs and others). They are solitary animals, remaining in families (females with young, sometimes the male). In the case of food, they are omnivorous animals; some are more specialized on plant foods (grass, berries, nuts), others on animal, feeding in particular on vertebrates or invertebrates including insects (bees, ants, termites, etc.). One species (polar bear) feeds exclusively on meat of large animals. The majority of species are quite strictly sedentary, while others (polar bear), roam widely the entire year (males) or part of the year (females with young).

In some species, all, or almost all populations (except extreme southern) hibernate (brown bear, white-chested bear, American black bear, *Ursus americanus*); in one species, only pregnant females live in dens (polar bear). Some species do not hibernate. They are monogamous*, however, they do not form permanent family pairs and the male does not take part in the care of offspring. There are 1, 2, or rarely 3, young.

They are mainly nocturnal, partially diurnal, or active throughout the day/night. Vision is weakly developed, hearing and smelling are very sharp. Mentally, it is one of the highly developed groups of the order; some forms in particular respond well to training.

The range of the family is vast and, in some respects, very unique. It is divided into two parts; the chief of which includes both land and open sea. The principal mass of the range occupies North America, Eurasia, the Arctic basin and a small area in northern Africa. A isolated section of habitat is found in South America. Bears are absent in almost all of Africa and in Australia, as well as on the greater part of the island region between Asia and Australia.

The established southern border of the northern part of the range in the New World covers the islands of Saint Lawrence, Saint Matthew**, Hall**, Nunivak**, and Pribilof**, the Alaska Peninsula (Bering Sea), and the eastern islands of the Aleutian ridge, westwards to include Unimak; then goes along the western coast of North America, including islands of Kodiak, Queen Charlotte, Vancouver and others and the northern part of the California peninsula, and crosses the mainland along Mexican territory. Here, the border goes southwards along the Sierra Madre system to the region of Durango and reaches the Tropic of Cancer, extending even a bit farther south. The border extends farther, along the coast of the Caribbean Sea to the Florida coast and northwards along the eastern coast of North America. Covering Newfoundland, it directs itself to the water at the southern tip of Greenland.

In the Old World, the limits of the range covered all of Europe, from northern Iceland and Great Britain, though without the islands of the Mediterranean Sea; the Atlas region in North Africa, Asia Minor, Syria and Palestine, Iraq, Iran, Pakistan, India, Ceylon,

*Sic; most, if not all, bears are presently considered promiscuous, not forming a pair bond of more than a few weeks—Sci. Ed.

**No records of bears from these islands—Sci. Ed.

Indochina, Malacca, Sumatra and Kalimantan (Borneo). Farther, it extended along the eastern coast of Asia, including Hainan, Taiwan, (absent on the Ryukyus), the Japanese islands, Sakhalin, Shantar islands, southern (Kunashir and Uturup) and northern (Shumshu and Paramushir) Kuril islands (absent on the remainder), Kamchatka and Karagin Island. On the Commanders they are absent. The range extended northwards to the high latitudes of the Arctic Ocean—apparently to the pole.

Within the outlined regions, there is no occurrence of the family over significant areas due to the unfavorable natural conditions (steppe, deserts, open tundra); in several regions they appear only accidentally (Iceland), or during migration, and do not reproduce (pelagic parts of the Arctic Ocean). In large territories they were exterminated (part of the United States, British Isles, some parts of Western, Central and Eastern Europe, North Africa, Japan and others).

402 In South America, the range occupies the higher (to 3,000 m)¹ parts of the Andes in western Venezuela, Colombia, Ecuador, Peru, and western Bolivia. Here, it was also reduced.

Everywhere, reduction of the range of the family represents only the result of their direct pursuit and destruction by humans. Based on all the characteristics of this unique family, it is an entirely recent, ecologically flexible and viable group.

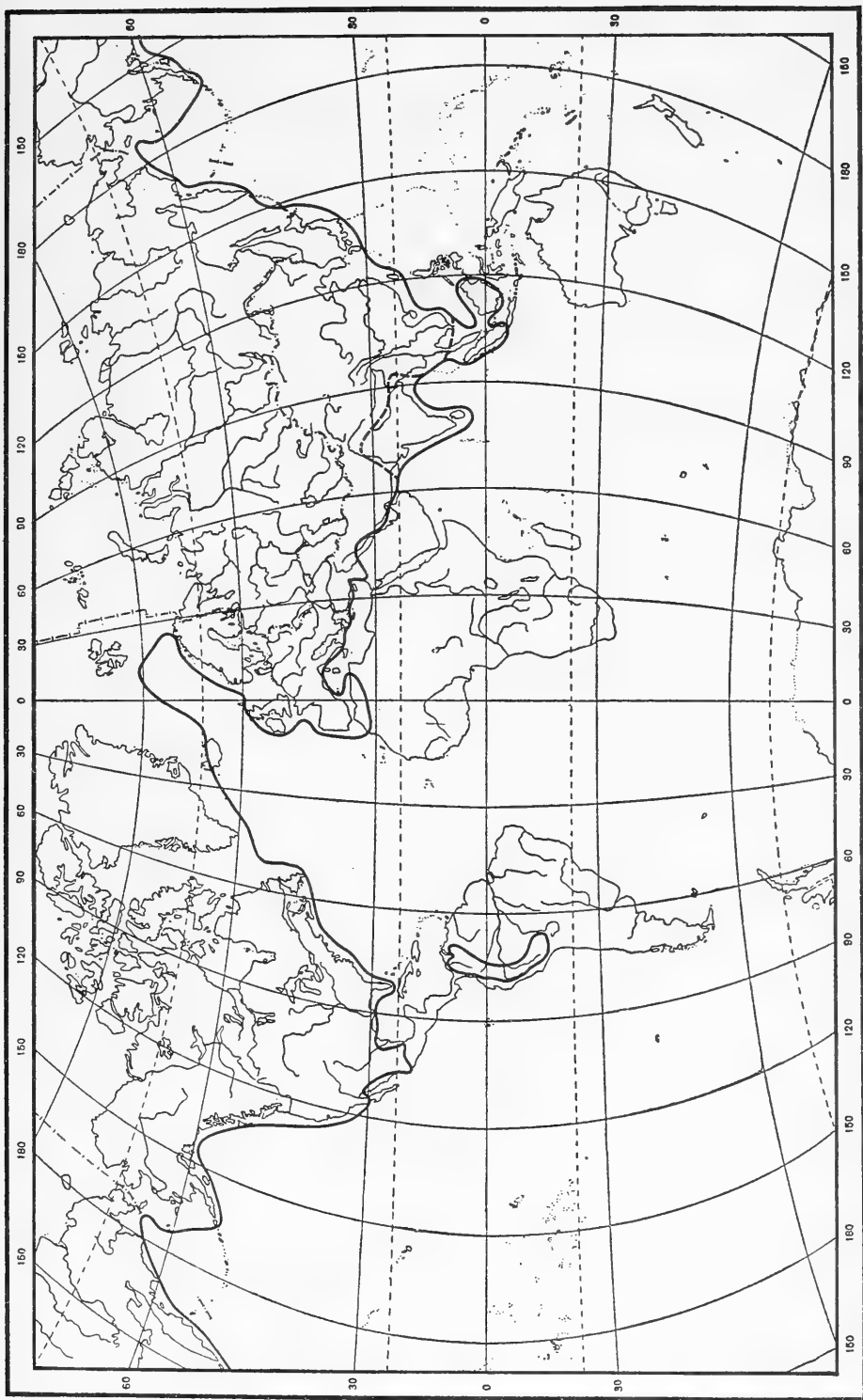
Within the limits of the superfamily* and groups of Canoidea, this family is well isolated and sharply differentiated from the others. For a long time, the composition of the family included the genus *Ailuropoda* (bamboo bear, or giant panda), producing a famous lack of clarity in determining the limits of the family. After excluding this genus from Ursidae and placing it in Procyonidae (raccoons), or grouping it together with *Ailurus* (panda, cat-like bear) in a special family, the limits of the described family became fully legible and natural**.

As a whole, the species of this family represents carnivores of a poorly specialized type. This is expressed both in characteristics of the skull and the dental system, and also in such characters as plantigrade limbs. In regard to its position among the recent families of

¹As was recently clarified, references to northern Chile were mistaken (Cabrera, 1957).

*In Russian original, mistakenly called "order"—Sci. Ed.

**Scientific opinion has recently swung back to the earlier view—Sci. Ed.



401 Fig. 149. Reconstructed range of the bear family, Ursidae, in North America and in the Old World. Solid line shows southern border of range, dashed line—reconstructed southern border of the genus of true bears, *Ursus* L., in Asia. Solid line in South America—range of the spectacled bear, *Tremarctos ornatus* Cuv. (V.G. Heptner).

the order, contemporary Ursidae reveal a significant relationship to the recent Procyonidae (raccoons). This is also partially indicated by the tale concerning the giant panda (*Ailuropoda*). Its relationship to modern Canidae (wolf family) is, apparently, not too close.

As regards its origin, the family is somewhat less ancient than Canidae, and the earliest forms appear in the middle or lower Miocene (*Ursavus*, Europe). Usually, the origin of the family is connected with the extinct subfamily Amphicynodontinae (Cynodontidae) of the family Canidae, which existed from the upper Eocene to the lower Pliocene. Among this group, the nature of originating material that gave rise to the recent Ursidae is usually given as *Cynodon*, *Dinocyon*, *Cephalogale* and several others. The divergence of bears from these truly flesh-eating carnivores was apparently determined most of all by their adaptation to eating plant foods. The dental system has changed correspondingly.

The development of bears proceeded, apparently, in Eurasia, whence the earliest forms of Ursidae are known, and also from which they are accepted as having derived. However, the old opinion, that in the New World this family appeared only in the Pleistocene, is wrong—from here representatives of the family are known from the lower Pliocene and, perhaps, even from the middle Miocene (*Ursavus*). It was never, one thinks, a family especially diverse and rich in species.

In internal systematic structure, this family is sufficiently homogeneous that subfamily groupings are not noted in it, and in this all investigators agree². In the handling of generic grouping, however, there is no agreement, and several authors even in our day put each species into an independent genus, or for 7 species, 6 genera (Pocock, 1941; Simpson, 1945; Ellerman and Morrison-Scott, 1951). This is an obvious exaggeration and the actual number of genera is undoubtedly less. This extreme point of view, and in general the strong division into genera, is explained by the fact that bear species are sharply differentiated from each other, and because morphological degrees of difference are great and clear. Among recent bears, forms whose

²The recent suggestion (Thenius, 1959; Thenius and Hofer, 1960) to divide the family into 2 subfamilies—Tremarctinae (American spectacled bear—one genus and species) and Ursinae (all other bears), based on paleontological considerations is incompletely argued, and is not accepted (see further, characteristics of the genus *Ursus*).

403 species independence might be doubtful and could be grouped together, are absent.³

In all, the family comprises 11–12 extinct, and 3–4 living genera.⁴ The recent fauna may include the following genera: *Ursus* including *Thalarctos*, *Euarctos*, *Selenarctos*, i.e. brown, [Asian] black and polar bears, as well as the American black bear; *Melursus* (sloth bear); *Helarctos* (Malayan bear) and *Tremarctos* (spectacled bear). The latter genus is closely related to the genus *Ursus* and, perhaps, may deserve to be combined with it.

Melursus is also closely related to *Ursus*. *Helarctos* is considered to be the most sharply deviant form—all remaining bears are closer to each other than *Helarctos* is to any of them. It seems as if to be contrasted to the others. Perhaps it might be more natural to divide the family into two genera—*Helarctos* with one species (*H. malayanus*), and *Ursus*, including all the remaining. At the same time, one may note a certain type of relationship between the genus *Ursus* s. l. and the genus *Helarctos*, through the white-chested bear. (*U. thibetanus*) (see description of white-chested bear), which make this proposed division not excessively sharp. Within the genus *Ursus* it is acceptable to create subgenera (see below). *Helarctos* represents the most specialized form (arboreal). The genus *Ursus* must be considered as a less specialized group; however, within it the degree of specialization is, in its turn, quite diverse (see description of genus).⁵

In the family there are, in all, 7 species, in the genus *Ursus*—4 (see characteristics of genus), in genus *Tremarctos*—1 (*T. ornatus* Cuvier, 1935—spectacled bear of South America); in genus *Melursus*—1 (*M. ursinus* Shaw, 1880—South Asiatic sloth bear) and in genus *Helarctos*—1 (*H. malayanus* Raffles, 1822—South Asiatic Malayan [sun] bear).

The practical significance of the species in the family is small. In different places, some cause definite harm to animal breeding, which is, however, inconsiderable. Almost all of them serve as objects of sport hunting, several of which in this sense are of great value (brown bear). Some have commercial importance for local needs or provide marketable skins (polar, brown bears). Numbers of a series of species

³The unlimited division of North American bears suggested by Merriam (1918), and which is still partly adhered to, is set to one side. It lies outside scientific zoology.

⁴According to Simpson, 14–18 extinct and 6 living.

⁵On the contrary, Thenius and Hofer (1960) consider *Helarctos* a less specialized form, and the brown bear, a specialized form.

have greatly decreased in connection with their pursuit, and hunting of individual species in parts of their range is found to be prohibited (polar bear). In some places, bears are considered as pests and are liable to be destroyed.

In the fauna of our country, there is one genus—*Ursus* Linnaeus, 1758, which comprises 25% of the genera of the family, and 3 species, i.e., about 43% of the species of the family. Bears constitute about 1% of the species of our fauna.

The range of the family covers almost the entire territory of the Union except the steppes and deserts and parts of the tundra. They are found on the Arctic Ocean.

They are game animals, objects of sport, as well as commerce. One species (polar bear) is considered endangered; hunting of the others is not restricted or is only restricted in a part of the distribution area (V.H.).

Key for Species Identification of the Bear Family

- 404 1(2). Color of fur white or with gray-yellow tint, bases of hairs white. Hairs on bottom of foot strongly elongated and much longer than on upper side. Upper molar teeth (last two teeth in tooth row; anterior one is first, and posterior is second) not large, total length less than distance between the anterior (first molars) of the right and left sides (Fig. 150) Polar bear, *Ursus maritimus* (p. 678).
- 2(1). Color different; bases of hairs black or brown. Hairs on bottom of foot not elongated, and in length not different from hair on upper side of foot. Upper molar teeth are large and elongated, their total length more than distance between anterior (first) molars of right and left sides.
- 3(4). Color from straw-brown to dark-brown. No sharply outlined clear white area on chest. On lower surface of fore foot, two large bare areas in addition to bare digital pads. Distance from middle of line joining postorbital processes to anterior end of premaxillae equal or nearly equal to distance from above-mentioned line to posterior point of occipital crest. Anterior edge of last upper molar lies anterior to anterior lower edge of orbit. Brown bear, *Ursus arctos* (p. 601).
- 4(3). Color is pure black or with very weak brownish frosting. On chest, sharply outlined clear white, half-moon-shaped field or,

in any event, extending in transverse direction. On lower surface of fore foot, in addition to digital pads, one large naked area, occupying whole surface of foot. On skull, distance from line connecting postorbital processes to anterior end of premaxillae considerably less than distance from above-mentioned line to posterior point of occipital crest. Anterior edge of last upper molar lies at level of anterior lower edge of orbit White-chested [Asiatic black] bear, *Ursus thibetanus* (p. 713) (V.H.).

Genus of Bears

Genus *Ursus* Linnaeus, 1758

1758. *Ursus*. Linnaeus. Syst. Nat. Ed. X, 1, p. 47. *Ursus arctos* Linnaeus.
1825. *Thalarctos*. Gray. Ann. of Philosophy, N.S., 10, p. 62, July 1825. *Thalarctos polaris* Gray = *Ursus maritimus* Phipps.
1825. *Thalassarctos*. Gray. Ann. of Philosophy, N.S., 10, p. 339, November, 1825. Substitute for *Thalarctos* Gray.
1855. *Tremarctos*. Gervais. Hist. Nat. Mammif. 2, p. 20. *Ursus ornatus* Cuvier. (Name used for *Ursus t[h]ibetanus*).
1864. *Myrmarctos*. Gray. Proc. Zool. Soc. London, p. 694. *Myrmarctos eversmanni* Gray = *Ursus arctos* Linnaeus.
1865. *Euarctos*. Gray. Proc. Zool. Soc. London, 1864, p. 692. *Ursus americanus* Pallas.
1896. *Thalassiarchus*. Kobelt. Bericht. Senkenberg. Naturf. Ges. Frankfurt am Main, p. 93, Substitute for *Thalarctos* Gray.
1898. *Ursarctos*. Heude. Mem. Hist. Nat. Emp. Chin., 4, pt. I, p. 17. *Ursus yesoensis* Lydekker = *Ursus arctos* Linnaeus.
1898. *Melanarctos*. Heude. Mem. Hist. Nat. Emp. Chin., 4, pt. I, p. 18. *Melanarctos cavifrons* Heude = *Ursus lasiotus* Gray = *Ursus arctos* Linnaeus.
1901. *Selenarctos*. Heude, Mem. Hist. Nat. Emp. Chin., 5, p. 2. *Ursus thibetanus* Cuvier.
1917. *Arcticonus*. Pocock. Ann. Mag. Nat. Hist., 20, p. 129. *Ursus thibetanus* Cuvier.
1923. *Mylarctos*. Lonnberg. Proc. Zool. Soc. London. p. 91. *Ursus pruinus* Blyth. = *Ursus arctos* Linnaeus (V.H.).

405 Dimensions large and very large.

Form and size of naked areas ("callosities") on lower surface of fore- and hind-feet vary in different species—in extreme cases, they occupy nearly their entire surface or, on the contrary, lower surface of foot almost entirely covered with hair.

Skull large and massive, with strongly or moderately developed facial portion and strong, relatively long, jaws. Zygomatic arches moderately broad and general outlines of skull proportional.

$$\text{Dental formula } I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{3} = 42.$$

Middle upper incisors always present, but first three premolars weakly developed and some of them frequently absent. They are usually shed with age, but sometimes do not develop a definitive system at all. More often, second and third premolars absent, sometimes also first. Fourth premolar always present. Therefore, dental formula individual in nature; in part age variation may

$$\text{take the form } I \frac{3}{3} C \frac{1}{1} P \frac{3}{3} M \frac{2}{3} = 38; I \frac{3}{3} C \frac{1}{1} P \frac{2}{2} M \frac{2}{3} = 34 \text{ and even}$$

$$I \frac{3}{3} C \frac{1}{1} P \frac{1}{1} M \frac{2}{3} = 30, \text{ i.e. deviating far from normal limit of family.}$$

Relative size of molars varies somewhat in different species.

Ears vary in size—of moderate length, distinctly protruding from fur, large and broad; or relatively small, slightly protruding from fur. Size of bare portion of nose and dimensions of lips vary in different species.

Pelage dense and long. Color of two species is very uniform, in one white with yellow highlights, the other pure black (polar and white-chested Asian black bear); one species is very variable as regards color—both individually and geographically it varies from dark brown to straw yellow (brown bear); one species (American black bear, *U. americanus*) has triphasic coloration, black, light brown and "blue"*. In one species, as a permanent qualitative feature, there is a large white spot on the chest (white-chested bear); lightening on the chest, sometimes a light collar appears in the form of an age character in young animals, and sometimes as an individual variation in brown bear.

*A forth, white, phase also occurs—Sci. Ed.

In the majority of forms, the posterior part of the body is highly developed and more massive; in one species—the anterior (white-chested bear). The genus comprises the largest forms in the family and order (see above, characteristics of the family and below, data on individual species), and species of moderate size, with a long body, about 180 cm and weight not more than 250 kg (American black bear).

The species of the genus are distributed in forest regions, in part in montane forests or in treeless mountains and plateaus, sometimes even in deserts, and extending into the tundra; one species is linked to ice and coasts of the Arctic Ocean, being a semiaquatic animal. Some species climb trees well, but in a restricted sense, these arboreal forms represent several other genera. They are omnivores, preferring plant forms, [but] one species (polar bear) is exclusively carnivorous. They are sedentary forms, [but] one species roams widely (polar bear). All species hibernate in winter.

The range of the genus (reconstructed) occupies the part of the general range of the family, being located in the Arctic Ocean, Greenland, North America, Europe, in northwestern Africa and in Asia except its extreme southern parts. Here, the southern range border of the genus crosses through Asia Minor, Palestine, Syria, Iraq, southern Iran, montane regions on the right bank [west] of the lower and middle Indus [river] along the Himalayas, and covering all Indochina, except the southern and middle parts of Malayan Peninsula (for more details, see description of range of brown and white-chested bear). During the past century, the range was strongly
406 reduced, and members of the genus are already absent in a large expanse. This applies to the greater part of North America, to Western, Central and Eastern Europe (European part of our country). Reduction has occurred locally in other parts of the range, but to a lesser degree.

In the genus there are 4 species—*U. arctos* Linn., brown bear; *U. thibetanus* Cuv., white-chested, or [Asian] black bear; *U. americanus* Pall., American black bear or *baribal*; and *U. martimus* Phipps, polar bear.

Contemporary representations of the species content of the genus given here were established only recently and are more or less widely accepted. However, in literature up to now, echoes of mistaken incorrect inferences still occur. The specific unity of all brown bears of Eurasia and also North America is sufficiently evident, and this was directly stated quite long ago not only in Russian, but also in the

Western European literature. However, even in 1931, when the contemporary broad concept of the species had not yet attained currency among our mammalogists, in the USSR the genus *Ursus* comprised six species (*arctos*, *piscator*, *mandschuricus*, *jessoensis*, *pamirensis*, *pruinus*; Ognev, 1931). For Central Asia two species occurred (*arctos*, *pruinus*; G. Allen, 1938).

In particular, the systematics of the American bears were misrepresented, and even now are often misrepresented. For only the American part of the range, Merriam (1918) separated 77 species, several with subspecies (total of 84 forms); one of these species was even separated in a special genus (*Vetularctos*). The "concept" of Merriam clearly lies outside of zoological science and generally cannot be taken into consideration, or has purely nomenclatural, even negative, significance. The species unity of American and Eurasiatic brown bears is, as was told, itself quite evident and was, more than once, confirmed in literature. Nevertheless, this "system" is still found reflected up till now in reports concerning the fauna of America (Anderson, 1946; Miller and Kellog, 1956).

Within the limits of the genus, the terrestrial form, the brown bear must, apparently, be considered the least specialized "generalized" one. The American black bear (*U. americanus*) is closest to it. They may be taken as one subgenus, *Ursus*. Another direction of specialization—greater climbing ability—is represented by the white-chested, or Asian black bear, which may be separated into a distinct subgenus, *Selenarctos*. The polar bear represents another direction of specialization related to water. They are usually accommodated under the subgenus (genus) *Thalarctos*. At the same time, if we leave to one side color and several other external features, the similarity between polar bear and brown is found to be very great, and a series of authors deny the basis for separation of polar bear into a special subgenus. The proximity of these species is also indicated by occasional cases of hybridization.

Different authors, more than once, confirmed the closeness of the Asian and American black bears—*U. americanus* and *U. thibetanus*. Some authors directly ascribe them to one genus (subgenus), *Euarctos*, placing them opposite the brown bears—*Ursus* s. str. This point of view was fully developed by G. Allen (1938). At the same time, as is in part clear from material to be brought out later, *U. thibetanus* itself represents a form quite strongly deviating from the purely "terrestrial" type of bear, while *U. americanus*, according to general

adaptive type—is a true “terrestrial” bear and is quite close to *U. arctos* in skull structure. Not only is its combination with *U. thibetanus* in one subgenus wrong, but also its separation in the subgeneric sense from the brown bear—*U. arctos*.

In relation to the Asiatic black bear, the generic name *Tremarctos* (Pocock, 1914) is also employed, which accentuates its proximity, in several respects, to the South American spectacled bear (*T. ornatus*). This, however, can hardly be accepted.

407 Within the boundaries of the USSR, there are three species: 1) brown bear. *U. (Ursus) arctos* Linnaeus, 1758; 2) polar bear, *U. (Thalarctos) maritimus* Phipps, 1774; and 3) the white-chested or [Asian] black bear, *U. (Selenarctos) thibetanus* Cuvier, 1823. They constitute about 43% of the species in the genus and about 1% of the number of species in our fauna.

In the USSR, the species of the genus occupy a large part of the country, except the Asiatic steppes, semideserts and deserts and part of the tundra (reconstructed range). Ranges of all species have decreased.

They are game and economically exploited animals in part considered as pests and pursued under law. One species (polar bear) is preserved by law (V.H.).

Subgenus of Brown Bears

Subgenus *Ursus* Linnaeus, 1758

BROWN BEAR

Ursus (Ursus) arctos Linnaeus, 1758

- 1758⁶. *Ursus arctos*. Linnaeus. Syst. Nat. Ed. X, 1, p. 47. Sweden.
 1788. *Ursus arctos niger*. Gmelin, Syst. Nat. Ed. XIII, 1, p. 100, Northern Europe.
 1792. *Ursus arctos griseus* Kerr. Anim. Kingd., p. 188. Germany.
 1820. *Ursus arctos minor* Nilsson. Skand. Fauna, p. 123, Very northern part of Scandinavia.

⁶Synonymy of European and North European forms of bear representing a pure literary and historical interest, given in short form. For details see Miller, 1912; Ellerman and Morrison-Scott, 1951; Couturier, 1954.

1824. *Ursus collaris* Cuvier et Geoffroy. Nat. Hist. Mamm., pt. 42, pl. 212. Siberia.⁷
1826. *Ursus isabellinus* Horsfield. Trans. Linn. Soc. Zool., 15, p. 334. Mountains of Nepal.
1827. *Ursus arctos brunneus* Billberg. Synop. faunae Scand., p. 15. Northern Scandinavia.
1827. *Ursus arctos myrmecophagus* Billberg. Ibidem, p. 16. Northern Scandinavia.
1828. *Ursus arctos formicarius* Billberg, Synop. faunae Scand., ed. 2, p. 16. Renaming of *U. a. myrmecophagus*.
1828. *Ursus syriacus* Hemprich et Ehrenberg. Symbol. Phys., 1, pl. 1. Lebanon.
1840. *Ursus cadaverinus* Eversmann. Bull. Soc. Imp. Nat. de Moscou, p. 11. Renaming of *U. arctos*.
1840. *Ursus longirostris* Eversmann. Bull. Soc. Imp. Nat. de Moscou, p. 11. Renaming of *U. formicarius*.
1851. *Ursus arctos* var. *normalis* Middendorf. Verhandl. d. Minerolog, Ges. zu St. Petersburg. Jahrg. 1850–1851, p. 74. Northeastern Europe.
1851. *Ursus arctos* var. *meridionalis* Middendorf. Ibidem, p. 74. Caucasus.
1851. *Ursus arctos* var. *beringiana* Middendorf. Ibidem, p. 74. Northwestern America.⁸
1851. *Ursus arctos* var. *kamtschatica* Middendorf. Ibidem, p. 74. Nomen nudum. Obviously, Kamchatka.⁹
1854. *Ursus pruinosus* Blyth. J. As. Soc. Bengal, 22, p. 589. Lhasa, Tibet.
1855. *Ursus arctos aureus* Fitzinger. Wiss.-pop. Naturg. d. Säugeth., 1, p. 371. Eastern Russia.
1855. *Ursus piscator* Pucheran. Rev. Mag. Zool., 7, p. 192. Petropavlovsk, Kamchatca.
- 408 1864. *Ursus arctos* var. 1 *normalis*. Gray. Proc. Zool. Soc. London, p. 682. Renaming of *arctos*.

⁷See "Note" in description of Eastern Siberian bear in the section "Geographic Variation".

⁸For type locality of this form and nomenclatural significance of name, see "Note" in description of Kamchatka bear in the section "Geographic Variation".

⁹Pagination in this work given according to separate reprint.

1864. *Ursus arctos* sub-var. *a. scandinavicus* Gray. Ibidem, p. 682. Scandinavia.
1864. *Ursus arctos* sub-var. *c. rossicus* Gray. Ibidem, p. 682. Nom. nud. Evidently, Russia.
1864. *Ursus arctos* var. *sibiricus* Gray. Ibidem, p. 682. Siberia.
1864. *Ursus arctos* var. 2 *grandis* Gray. Ibidem, p. 684. Northern Europe.
1864. *Ursus arctos* var. 4 *stenorostris* Gray. Ibidem, p. 685. Poland.
1864. *Myrmarcos eversmanni* Gray. Ibidem, p. 695. Norway.
1867. *Ursus lasiotus* Gray. Ann. Mag. Nat. Hist., 20, p. 301. "Inner part of Northern China". Located more exactly: eastern part of Manchuria.
1873. *Ursus leuconyx* Severtsov. Vertik., gorizont. raspr. Turkest. zhivot. Izv. Obshch. Lyub. est. antrop. etnogr., 8, No. 2, p. 79. Valley of upper Naryn, Tien Shan.
1833. *Ursus lagomyarius* Przevalski. Przheval'skii Tret'e putesh. v Tsent. Asii [Third journey in Central Asia]. p. 216. Mountains of Kuku-Shili, Eastern Tibet (35° N. Lat., 96° E. Long.).
1883. *Ursus hypernephes* Przevalski. Przheval'skii, Ibidem, p. 216. Substitute for *U. lagomyarius* Przew.
1897. *Ursus arctos yesoensis* Lydekker. Proc. Zool. Soc., London, p. 422. Hokkaido Island, Japan.
1898. *Ursus mandchuricus*. Heude. Mém. Hist. Nat. Emp. Chin., 4, p. 23–24, pl. 7. Near Vladivostok.
1898. *Melanarctos cavifrons*. Heude. Ibidem, 5, p. 1. Tsitsikar, north-eastern Manchuria.
1913. *Ursus arctos lasitanicus* Satunin. Tr. Obshch. izuch. Chernomorsk, poberezh'ya, 2, p. 27. Sukhumskii area.
1916. *Ursus arctos* var. *caucasicus* Smirnov., Zap. Kavk. Muzeya, ser. A, No. 4, p. 117. Passanaur on the Georgian Military Highway (southern slope of Main [Caucasus] Range).
1916. *Ursus arctos arctos* L. natio *dinniki* Smirnov. Ibidem, p. 122. "Chatakh, Borchalinsk. u. [county], Tiflissk. guber. [governance]".
1924. *Ursus arctos yeniseensis* Ognev. Priroda i okhota na Ukraine [Nature and Hunting in the Ukraine], 1–2, p. 112. Maina, tributary of Ungut R[iver], vic. of Krasnoyarsk.
1924. *Ursus arctos baicalensis* Ognev. Ibidem, p. 112. Kudaldy, Trans-Baikaliya.

1924. *Ursus arctos kolymensis* Ognev. Ibidem, p. 112. Zabortsevo on the Kolyma [River].
1924. *Ursus yessoensis* Ognev. Ibidem, p. 112. In place of *yessoensis* Lyd. 1897.
1924. *Ursus pamirensis* Ognev. Ibidem, p. 111. Pamirskii post, Pamirs.
1925. *Ursus arctos persicus* Lönnberg. Fauna och Flora, 1, p. 28. Mezanderan, N. Iran.
1925. *Ursus arctos smirnovi* Lönnberg. Ibidem, p. 28. Northern slope of Main Caucasus Range (V.H.).

Diagnosis

Dimensions large to very large. Color normally brown, of different intensities, but individually, and in part, geographically very strongly variable—from straw-yellow to almost black. On lower surface of forefoot, in addition to five digital callosities (pads), there is a large transversal anterior callosity and a separate small rounded posterior one located nearer outer edge of foot. Facial part of skull relatively long, last upper molar broad and elongated, considerably larger (nearly double) than anterior; last lower molar relatively large, noticeably constricted posteriorly (V.H.).

Description

The brown bear is a massive, very heavy bodied animal. In all its parts, it is quite proportioned, although at first glance, it appears very "clumsy". This impression is also due to the fact that movement of the animal is usually slow and unhurried. Posterior part of body—croup and thigh—more massive than anterior; however, fore limbs large, strong, and no such disproportionality between anterior and posterior parts of body as in polar bear. Above-mentioned unconformity is concealed in that withers are high, and its hair very long, giving the impression of a sort of "hump". This is also emphasized in that the bear carries the head lowered and raises it only while listening and sniffing.

Head large and heavy, with broad and high forehead and ears quite tall and set apart. It is only moderately elongated, and seems less elongate than black and polar bears, but is relatively larger, more massive and heavier. Ears comparatively small, rounded, and in

animal in winter pelage, basal half hidden in fur of head. Eyes very small, dark; bare part on tip of nose quite large, black. Lips black, large, quite loose, and like nose, very mobile (protrusible). Tail very short and entirely hidden in fur. Claws very large and curved; those on fore-limbs considerably longer than on hind-limbs; length of largest may attain 5–6, or even 7–10 cm along curve. Their color is blackish-horn or dark with lighter tip; in some forms, light-horn over entire extent, or on greater part.

On lower surface of hind foot, there are 5 well developed, bare digital pads; base of free parts of toes covered with hair. All remaining surface of sole bare and itself represents metatarsal callosities (pads) united into one large area. Borders between them denoted by fold beginning at outer part of sole. On lower surface of forefoot, digital pads and large transversal anterior callosity in anterior part of metacarpal region well developed; posterior to this, nearer exterior side of sole, lies a small rounded callosity. Additional, ill-defined, small secondary posterior callosity occurs closer to interior side of sole.

Winter fur, especially in northern animals, very thick and long. Length of longest hairs in large forms reaches 11–12 cm (on the withers). Comparatively, general dimensions of hairs thin, but fur quite rough to the touch; hairs flexible with silky luster, and as a whole, the coat is very beautiful. Pile* of skin ill-defined, and on living animal, full winter coat appears to flow when animal moves (walks).

Summer, i.e., transitional fur (molt is once per year) is much shorter and sparser. Apparently, in very old and large bears, fur is shorter in comparison to that of younger, smaller animals. Length and density of fur varies geographically. Fur of southern bears—Caucasian, and especially Trans-Caucasian and Middle Asian—sparser and coarser, of northern [bears] denser, longer, and more silky. Fur of bears of the Far East and Siberia is especially good, and among them, particularly that of Irkutsk and Trans-Baikaliya.

Color brown, generally homogenous over whole body. “Usual tone of winter coat of adult Middle Russian bear is as follows: whole
410 back covered by hairs of dark and dark-brownish tone admixed with various amounts of black. On lower part of back and on thighs, tone of fur is darker, more blackish. On shoulder region, color is, on the

*Directional “set” of hairs on skin—Sci. Ed.

contrary, often lighter, possessing a slight reddish tint as a result of the development of this color on the very tips of the hairs. Ears dark brown and their intense color sharply distinguishes them from background of lighter forehead and upper part of cheeks, which are of more reddish-straw color. Between the eyes, fur becomes darker again, and merges into dark-brown or blackish-chestnut. This intense tone covers the whole nose, around eyes, and lower part of cheeks. Chin is also dark; on neck (below), a weak admixture of rusty fur is observed; belly is dark brown. Limbs are darker than back; the nearer the end of the feet, the blacker the intensity of fur color becomes. Feet are dark blackish-brown. Length of hair in region of middle back is about 55 mm, in shoulder region and between shoulder blades, about 85, and on posterior part of back—about 90; on thighs—85, and in middle of forehead, about 32 mm.

Color of individual hairs in region of middle back is as follows: their deep base is dark-ashy-gray-brownish; from this basal portion extends a wide, intensively-brown zone, and the extreme hair tips are rusty-brownish. This color of the hair tips is weakly developed in the middle back, and hence the general tone of the back is darker than the sides, where the rusty tips of the hair are wider, and protrude more noticeably externally. On the lower part of the back, rusty tips are completely absent, which modifies it to a dark color. The hairs of the very short tail are dark-brownish-blackish" (Ognev, 1931).

Individual variations from this widespread type of coloration are comparatively small and are expressed only as darkening, lightening or reddening of the general type. In extreme cases, Middle Russian animals have a very dark, nearly blackish-brown color; in rare cases, almost black or, on the contrary, light reddish-brown.

In some regions, individual variation is greater, and very dark or very light animals are found equally—in extreme cases, golden-light-pale yellow, or nearly straw-yellow. In other regions the whole gamut of colors shifts in the direction of lightening. Sexual differences in color are absent. Color of young is variable and in one litter there may be both dark and light individuals. Generally, they are lighter than are adults. In many cases in young bears, two well developed white spots, not sharply outlined, are found on the neck and nape. Quite often, these spots form a light collar. This latter, in rare cases, is retained in subadult animals and, as a rare exception, (more often in Central Asia) even in adults. By the second year, young bears are

generally lighter in color than adults and old animals, and among them, very light individuals are often found.

Geographic variation in color is quite strongly expressed in some parts of the range. In separate areas, there is a prevailing tendency towards variation of the usual color intensity to one or the other side. Thus, bears of the Caucasus, and particularly the Trans-Caucasus and Middle Asia, are lighter than northern ones; contrast in color of the limbs and body changes, appearing to darken in the region of the withers, etc.

Skull of brown bear large and massive, with well developed crests and general sculpturing. Sagittal crest in adult animals is developed on frontal bones, and at place it unites with occipital crests; a large posteriorly directed projection is formed. Postorbital processes large. Facial region large and strong; its length approximately equal to that of brain case—distance from anterior point of premaxillae to line uniting ends of postorbital processes equal or almost equal to distance from above-mentioned line to posterior point of dorsal protrusion of occipital and sagittal crests. Distance from anterior margin of orbit to anterior internal point of premaxilla greater than width of frontal area between outer points of postorbital processes.

Anterior part of rostral region comparatively wide—its width above canine teeth usually not less or hardly less than width across preorbital foramina. Frontal area wide, sharply demarcated posteriorly by anterior branches of sagittal crest, and flattened or concave in longitudinal direction. Braincase relatively small, not swollen, and elongated. Zygomatic arches strong, widely separated. Mastoid processes very large, articular [processes] massive and large. Nasal opening relatively large and wide. Lower jaw massive, elongated, with large coronoid process and very massive articular condyle.

Individual variation of skull very great. Skull may be relatively narrower and more elongated, or broad with stronger or less pronounced crests and general sculpturing; form, dimensions, and surface (concave, flattened) of frontal area, size of postorbital processes, steepness of transition from nasal region to the forehead, entire upper line of profile, and a series of other characters may vary. Particularly characteristic of adult animals is that skulls may be of two types. One—"normal"—is large, with sharply defined protuberances, crests, etc., and with compressed brain case; the other is of smaller dimensions, with more weakly defined protuberances, crests, etc., and a relatively less compressed and more swollen braincase; on the whole

a more "infantile" type. Such skulls are encountered, apparently, throughout the whole range, but more often in several places therein (see below).

Sexual differences in structure of the skull are well pronounced. In the female, the skull is smaller and not so massive, crests and protuberances of the skull are weakly developed, braincase is relatively less compressed, zygomata not so massive and not so widely separated, and the nasal opening is relatively narrow.

Age variation in the skull is very great and lies in relative reduction of the braincase, increase of facial part, development of crests and processes and widening of the zygomatic arches.

Geographic variation of the skull is quite significant, but reveals itself chiefly in general dimensions. Structural differences are more weakly developed and express themselves mainly in the degree of strengthening of protuberances, crests, etc., of the skull; in the lesser or greater elevation of the frontal region, general relative elongation

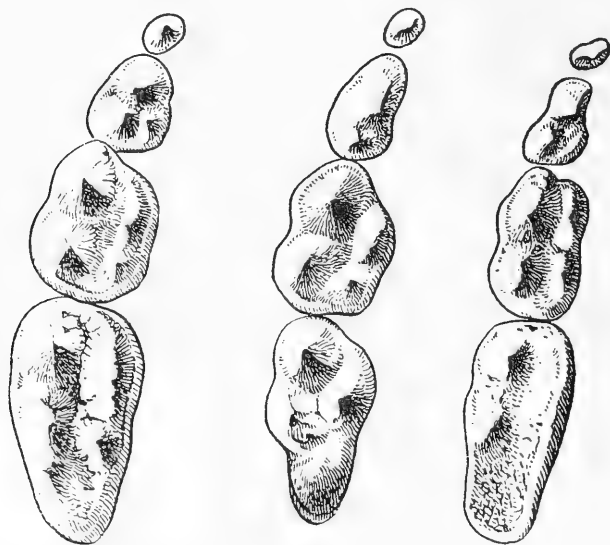


Fig. 150. Upper [cheek] teeth of brown bear, *Ursus arctos* L. (left), polar bear, *Ursus maritimus* Phipps*, and white-cheested bear, *Ursus thibetanus* G. Cuv. Sketch by N.N. Kondakov.

*Sic; should be Phipps—Sci. Ed.

of the skull, and in width of the zygomatic arches. The relative number of individuals in a population possessing the described "infantile" skull is also significant.

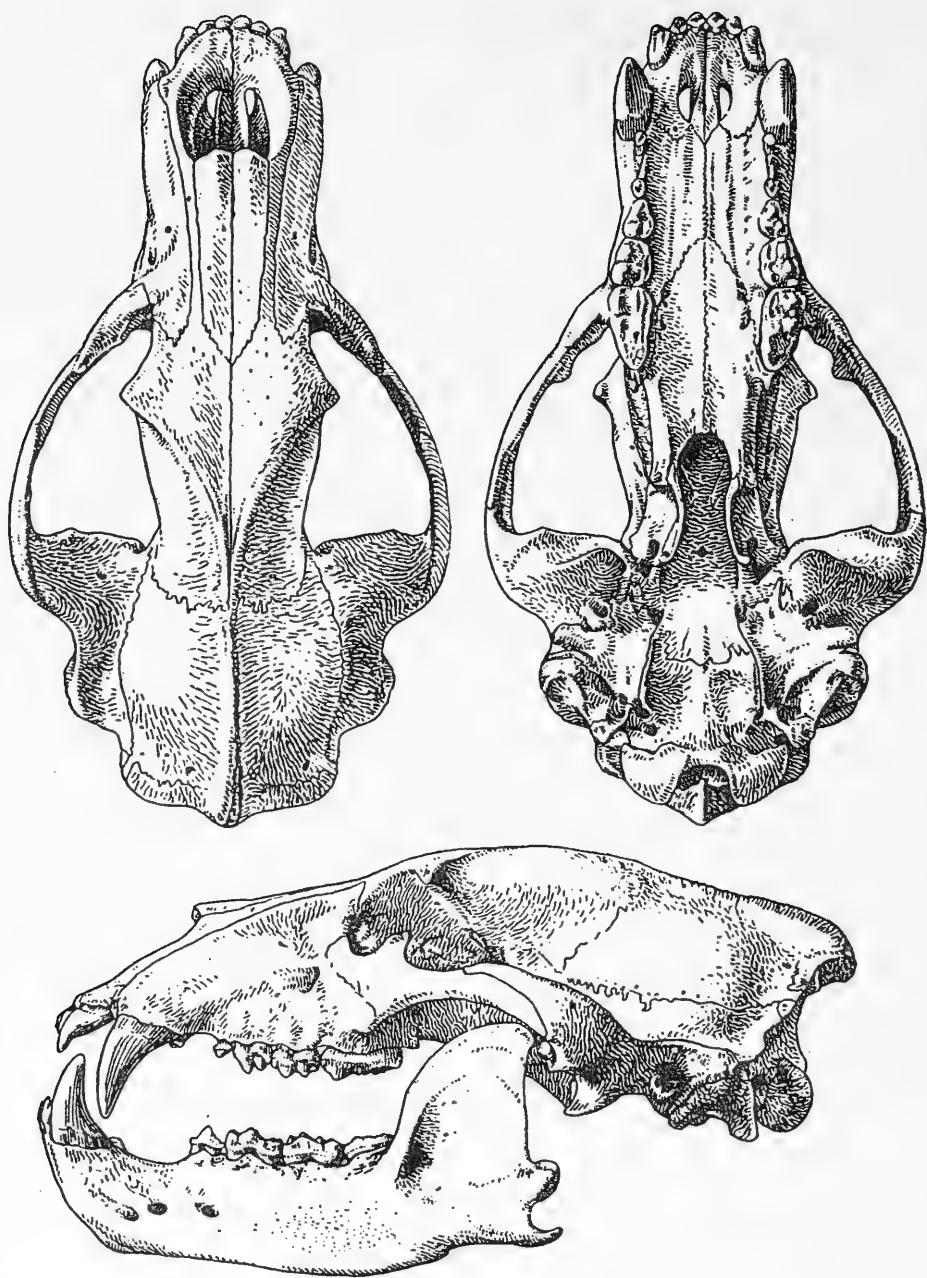
Teeth very strong. Incisors relatively big, canines large, with lower ones strongly curved backwards. First three premolars of upper jaw underdeveloped, single-crowned, with one root. Usually, first of these teeth lying adjacent to canine retained with age, as well as third, shifted towards fourth premolar. Second, which is smaller than first and third, very often absent in adult animals. It usually falls out early, leaving no trace of its alveolus in the jaw. More rarely, first or third or even both fall out and their alveoli grow over. Fourth premolar much larger than others, with two roots and never falls out—rudiments of premolars, entirely characteristically for family in general, do not encroach on it.

Second molar very large—broad and elongated. Its length approximately equal or slightly less, sometimes even more than, length of first molar and fourth premolar together. It is approximately twice as large as first molar, and length of both molars usually more than width of palate between first molars (Fig. 150).

In lower jaw, first three premolars also very weak. Second one absent in majority of cases, its alveolus usually not evident, first and third also often fall out. Fourth premolar* always present and has two roots; the first molar elongated and relatively narrow, second approximately equal to it in length, but wider and more massive. It is largest molar. Third molar shorter than the second, in anterior part it has same width, posteriorly, somewhat narrower than [second]; it [third] has rounded-oval outline; anteriorly, somewhat wider; ratio of length to width approximately 1 : 1.5.

Brown bear, equally with polar bear, are the largest species of Recent terrestrial carnivores. Its dimensions fluctuate very greatly according to sex, age, individual and geographic variation, and also by season. Moreover, accurate data concerning size of the bears are quite scarce, with many contradictions. Therefore, characterization of the species in this respect is difficult. Body length of old males of the largest races (Far Eastern, northwestern North American) reaches 245–255 cm, height at withers—120–135 cm. Weight reaches 500, 525, and 640 kg. A large bear, standing on the hind feet, has a "stature" of 2.73–3.00 m.

*Misprinted "molar" in original Russian—Sci. Ed.



Such huge animals significantly exceed the average weight level of their populations. They are usually very old animals, growing and surviving under very favorable conditions (for example, preserves) and particularly strongly fattened in winter. The weight of "normal" large males, as a rule, does not exceed 250–300 kg, or somewhat more (320 kg—20 puds). Higher weight in Europe and Asia (except the Far East) constitute rare exceptions, and in the Far East are met with very rarely¹⁰.

The smallest races of bears have, apparently, a body length of 130–150 cm, and a weight of about 56–80 kg.

414 Variation in dimensions of animals in one or another population depend to a considerable extent on the intensity of hunting in a given region. Bears grow for a long time, and where they are much hunted, the animals do not grow to maximum size, and in such population, the proportion of young small bears is relatively great. This occurs locally, for example, in the European part of the Soviet Union. Large dimensions of Siberian and Far Eastern bears are explained, not only by natural geographic variation of the species, but in part evidently by the above-mentioned situation.

¹⁰It must be taken into consideration that animal weight is often exaggerated as hunters usually estimate it "by eye"—very rarely is it possible to get accurate weight of a dead animal. They are usually not very interested because they do not deal with this account of the trophy. According to recollections of our famous hunters and sportsmen of the end of the past and beginning of the present century, S.A. Buturlin, G.I. Polyakov and F.F. Shillinger, a weight of 500 kg (30 puds) is very rare (V.G. Heptner).

Records exist (Ognev, 1931; Couturier, 1954) of bears weighing 640 kg (40 puds, Kamchatka) and 550, 589, and 750 kg (Alaska). Finally, one animal from Kodiak Island, living in the Berlin Zoological Garden in 1937 had an unbelievable weight—1200 kg. If all of these figures are true, then they belong to giants, which occasionally are encountered among many species of mammals.

Very often, not only in popular, but also scientific literature, measurements of North American bears are exaggerated, especially from the northwest where the largest forms of the New World actually live. According to the most recent data, "large grizzlies" weigh 250–300 kg (Couturier, 1954); animals from Alaska (very large form *middendorffii*) have a body length of 180–190 cm (Bee and Hall, 1956); according to Anthony (1928), body length of American bears is 180–255 cm, shoulder height is from 90 to nearly 120 cm, weights from 158 to 410 kg and in "park" animals up to 525 kg. Only Burt and Grossenheider (1952), followed apparently by Trautman (1963), indicate body length of the form *middendorffii* as about 240 cm., shoulder height 120–135 cm and weight to 681 kg (1,500 English pounds) and more. Our Far Eastern bears correspond in their dimensions to the large American races (see section "Geographic Variation").

Sexual differences in measurements are pronounced—females are always considerably smaller than males. Their average weight consists, apparently, of not more than 75% of that of the males, and evidently usually less (in the Pyrenees, the largest known weight of a female bear is 250 kg, of a male—350 kg; Couturier, 1954).

Weight of animals changes greatly by season. Lowest weight of all is observed in spring after winter hibernation, and in autumn, in a well-fed animal, fat may constitute 20% and more of total weight. Especially fat bears occur along the shores of the Pacific Ocean, fattening on salmonid fishes. Age changes in measurements and weights of bears are extraordinarily great. This is partially explained by the fact that young are born very small and have a weight of 250–400 g (Europe), or 450–625 g (large American forms; Couturier, 1954). This constitutes approximately 1/500, 1/600 of the weight of adult animals.

Dimensions of the skull of bears living in our country (excluding subspecies differences) are as follows: greatest skull length of adult males, 311–455 mm; of females, 275–397 mm; condylobasal length of skull of males, 261–418 mm; of females, 258–373 mm; zygomatic width of males, 175–277 mm; and of females, 147–247 mm. Sexual variations in skull dimensions are relatively less than in general [body] measurements (V.H.).

Systematic Position

Among some features of skull structure, the brown bear manifests characters of quite high specialization. Among those are attested the relatively elongated facial region, comparatively small brain case, strongly developed crests, most of all the sagittal, and general sculpturing of the skull. In this regard, the subgenus *Selenarctos* (white-chested bear, *U. thibetanus*) has less specialized characters. The shortened facial region, relatively voluminous brain case, less developed crests, and several other characters, give the skull of the white-chested bear a more infantile appearance in a sense.

At the same time, some features of body structure, for example, the relationship of fore and hind limb measurements, development of the proximal parts of the feet, and several others, allow us to see in the [Asian] black bear a more specialized climbing form than in the almost purely terrestrial brown bear. It is more specialized as an herbivorous form. The above-indicated characters

of skull structure may be associated in part with the generally smaller dimensions of the animal. These statements allow us to consider the brown bear as qualitatively the "central", more generalized form of the genus¹¹. The polar bear itself is considered to be derived from the brown, and in any event, stands closer to it than the white-chested bear (V.H.).

Geographic Distribution

Eurasia, on the north to the limits of woody vegetation, on the south to the Himalayas, Mediterranean Sea, and northwestern Africa, North America west of longitude 90° W. Long., in the north nearly to the northern extremity of the continent, and south to Mexico.

Geographic Range in the Soviet Union

Range (reconstructed) occupies the entire forest, and in part the forest-steppe and steppe zones, eastern tundras, the Caucasus and montane regions of Middle Asia. It constitutes a considerable part of the range of the species (about half), and occupies the greater part of the territory of the USSR.

Within the USSR, the range consists of three, more or less isolated, principal sections—the main European—Siberian massif, associated with forest and in part, forest-steppe and steppe; the Caucasian, mainly the montane forest region; and the Middle Asian part, where bears inhabit mountains that are partially unforested. All three sections join, or were joined in the past, in the south, beyond the borders of our country; the Caucasian with the European-Siberian through Asia Minor, the Middle Asian with the other two through Iran, Afghanistan and China. During the historical period, the range of the bear in our country changed greatly as a result of its reduction. In previous times, there was less isolation of the separate parts of the range in our [country], including the European-Siberian and the Middle Asian parts. Evidently, such contact occurred to the east of Kazakhstan, and in ancient times also through the western Cis-Caucasus.

¹¹This conclusion is preliminary. It is probable that the American black bear must be considered the "central form". The solution to this question is possible only through a complete revision of all bears, the system of which, as stated, cannot be considered accurate.

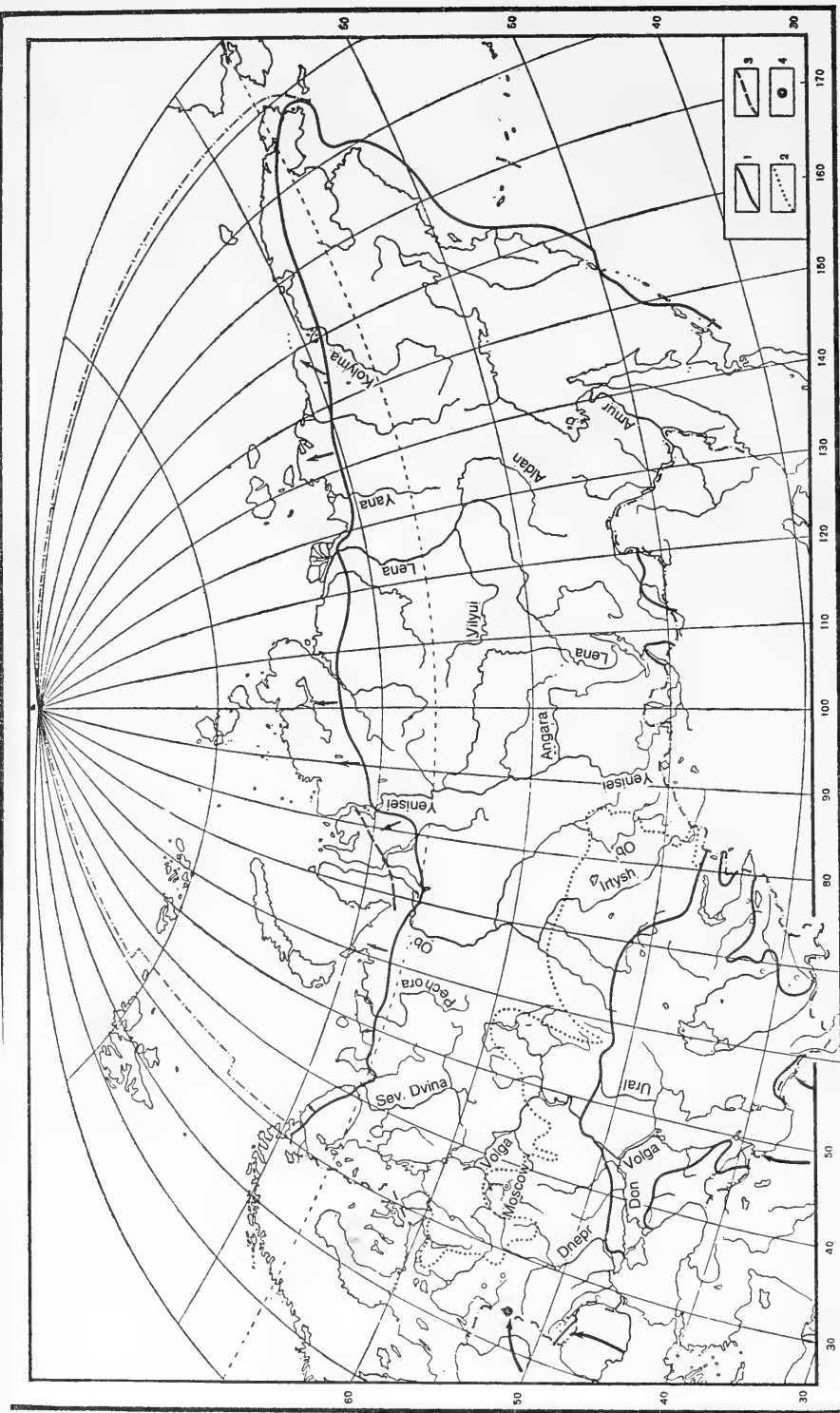


Fig. 152. Range of brown bear, *Ursus (Ursus) arctos* L., in USSR (V. G. Heptner):

- 1—Border of reconstructed range; 2—Southern border of distribution in western Siberia and European part of USSR at end of 50s of the twentieth century and in 1960; 3—Northern border of regular transgressions into tundra of western Siberia; 4—Isolated point of occurrence in Belovezhsk Forest. Arrows in north indicate far limits of transgressions to tundra; in south—isolated regions of occurrence in Carpathians, Talysh and Kopet-Dag.

The range has changed significantly in the past ten years, and is changing quite quickly before our eyes. For this reason, a more or less precise determination of the distribution limit for the animal is, in many cases, impossible. Moreover, in some regions in the north, bears roam very widely and delimiting the area of normal permanent occurrence, the region of regular transgressions, and the region of rare, especially long transgressions, is difficult.

The northern border of bear distribution in the European-Siberian part of the range, generally speaking, is associated with the northern border of the forest and forest-tundra. In it the bear is rare, although in some parts it remains permanently, and regular transgressions occur. Almost everywhere, the animals go into the tundra, mainly its southern part, but in some places they penetrate quite far north.

On the Kola Peninsula, the region of permanent occurrence of the animal does not reach the Murmansk coast. The border passes along the latitude of Murmansk and extends to the mouth of the Ponoï on the eastern shore of the peninsula. Wandering animals go into the tundra in the summer time and to the north and east they reach the seacoast. On the Solovets Islands, the bear is absent, and probably was never present. Farther to the east, the border includes the extreme lower reaches and the mouth of the Mezen', the southernmost part of the Kanin (mainly transgressions) and goes along the southern border and southern extreme of the Timansk, Malozeml'sk and Bol'shezemel'sk tundras, reaching the extreme lower Pechora. In the area between the Kanin and Pechora, bears in summer go far into the tundra and even reach the seacoast.

In the northern Urals, the bear normally lives below 65° and is met with in the tundra up to 67° N. Lat. Farther east the border goes to the extreme lower reaches and the mouth of the Ob', passing it at approximately the latitude of the Arctic Circle at Salekhard. From here, the border takes its direction along the southern shore of Obisk Bay or slightly before it. In any event, in summer time the animals live along the coast itself. Farther to the east, the border of the area of permanent occurrence is an arc-shaped line, slightly ascending to the north, going to the mouth of the Taz on Tazovsk Bay. In the Taz-Yenisei interfluvium, the border ascends still farther to the north, including the Great and Small Khetta [rivers], and goes on to the Yenisei at Dudinka (69°30' N. Lat.).

In the expanse between the northern Urals and the Yenisei, the northern border of the area of irregular occurrence and transgressions crosses the sources of the Usa (about 68° N. Lat.), somewhat north of Yarro-to Lake and across Cape Kamenny (about $68^{\circ}30'$ N. Lat.) on Yamal, along the northern shore of the Tazovsk Peninsula (about 69° N. Lat.), across the head of the Gyda river on Gydansk Peninsula ($70^{\circ}30'$ N. Lat.) and ascends on the left [west] bank of the Yenisei to the level of Tolsty Nos [cape] ($70^{\circ}15'$ N. Lat.) and even further north (Shirokaya Bay). The outlined area occupies not only the whole forest-tundra, but also a considerable part of the southern tundra.

From the mouth of Yenisei, the border directs itself to the mouth of the Khatanga, covering the basin of Pyasinsk Lake ($69^{\circ}30'$ N. Lat.), the basin of the Khetta and the left tributary of the Dudypa (Kamennaya) to $71^{\circ}30'$ N. Lat. and extends to the Khatanga at $72^{\circ}30'$ N. Lat. (Novaya river). Thus, on Taimyr, the area of more or less regular occurrence and short transgressions (their delineation is difficult) goes farthest to the north and includes true tundra. Here, their migrations also extend farthest to the north.

Farther to the east, the border is very poorly elucidated. It is possible to consider that it goes along the extreme lower reaches of the Olenek, Lena, Omolon, Yana, Indigirka and Kolyma, and on the latter, proceeds to the mouth. On the Lena, bear dens, though rare, occur at Bulun ($70^{\circ}30'$) and Kumakh-Surt ($71^{\circ}30'$) not far from the beginning of the delta. Transgressions of the bears occur northward—at Bykovsk Cape (72° N. Lat.).

In all the above-mentioned extent of Middle and in part East Siberia, the border of the range generally proceeds along the border of the krummholz and tundra, so that the krummholz also serves as the region of the normal occurrence of the animal, while the area of tundra is mainly that of summer transgressions¹².

Eastward from the Kolyma, the border of the range goes considerably to the north of the tundra border, proceeding along the northern slope of the Anadyr range and extending to the Pacific

¹²The border of the range in the European part of the Union and in Siberia is mainly from Middendorf, 1867; Pleske, 1887; Flerov, 1929, 1933; Yakovlev, 1930; N. Naumov, 1930; S. Naumov, 1931; Ognev, 1931; Tugarinov, Smirnov and Ivanov, 1934; Adlerberg, 1935; Heptner, 1936; Kolyushev, 1936; Shvarts, Pavlinin and Danilov, 1951; I. Laptev, 1958; Belyk, 1953; V.N. Skalon and other sources.

Ocean somewhere in the middle part of the Chukotsk Peninsula (north of Krest Gulf).

Summarizing the previous data, it is believed that the northern border of normal habitat occupied by the bear goes (except for northeastern Siberia) along the northern border of the forest. However, in summer, animals (mainly males, apparently) roam quite widely and actually wander everywhere in the southern tundra, and strictly speaking, the actual border is located in this zone. In addition to this regular occurrence there are, in places, much farther transgressions of animals to the north for distances of tens and even hundreds of kilometers. In addition to the above-mentioned transgressions in the European part of the country and in western Siberia, especially distant transgressions into Taimyr to 73° and even to Taimyrsk Lake at 74° , and to the ocean in Yakutiya, are known.

The shore of the Pacific Ocean, to the southern border of the state, forms the eastern border of the range. Bears exist on Karaginsk Island, Shumshu and Paramushir on the northern Kurils and on Kunashir and Iturup of the southern [islands] (absent on remainder), on Sakhalin and Shantar islands. The northern and eastern borders of the range at the present time are the same as described and apparently have not changed substantially in any way in the last 100 years. In contrast, on Shumshu Island the bear has recently disappeared (Podkovyrkin, 1960).

The southern (reconstructed) border of the range in our country extends from the Pacific Ocean to the Altai and Tarbagatai, coinciding with the state boundary. Animals are absent and never were present, apparently, in the steppes of southeastern and probably, 418 southwestern Trans-Baikaliya. This border has not been subjected to significant change during the past 100 years.

From the Tarbagatai [range], the border generally proceeds toward the northwest, crossing the steppes of Kazakhstan to the Urals. It envelops, from the south, the Kazakh *melkosopochnik* [small hills] (Kazakh folded country), passing somewhere in the middle between Karkaralinsk and the northern shore of [Lake] Balkhash. Farther, crossing the Nura and the upper Ishim, the border encloses, from the south, the Kokchetavsk upland and passes westward to the upper Tobol, crossing it a little south of Kustanai (Ara-Karagai pine forest). Thence, the line of the border surrounds, from the south, a section occupied by the animal in the former

Troitsk county (Kaban-Karagai), goes on to the upper Ayat (tributary of the Tobol entering above Kustanai), and thence to the valley of the Ural, approximately at Orsk. The occurrence of the bear here is, in particular, recorded at Rossypnaya and Nizhne-Ozernaya (below Orenburg). The bear was distributed along the Ural valley to Ural'sk.

In these demarcated steppe and forest-steppe districts of Kazakhstan, the bear was distributed only sporadically. It lived in pine forest islands, cut-over land and montane sections (*melkosopochnik*) with woody and shrubby vegetation, and even without it. The bear still inhabited some parts of Kazakhstan in the 18th century (sources of the Nura south of Karkaralinsk, Ara-Karagai), and in other, it existed up to the beginning of the 20th century (Sandyktau, Kokchetavsk mountains around Borovyi). It cannot be excluded that in more ancient times the bear was distributed farther south than is now known and described here. Thus, it is not excluded that it inhabited Ulutau, although there is no information on this, and several other places to the south. It is interesting that all of the border demarcated goes through the steppe zone, in the east, very near the border of semidesert and desert zones.

The area inhabited by the bear in Kazakhstan itself represents the southern extreme of the middle- and western Siberian part of the range. However, in the steppe and forest steppe of western Siberia the bear has not been present for a long time, and it is difficult to explain how it disappeared in this region. Apparently, in Kazakhstan, the bear still existed at some points even when it did not exist in considerable areas farther north.

The recent (1950's) the line of the southern border of the range in western Siberia cannot be delimited with sufficient accuracy due to inadequate information. In the Altai, the animals live everywhere, including the extreme south—the basin of Markakol' Lake and to the Zaisan depression (in the depression itself, it is absent), in Narymsk range and in Kalbinsk Altai (left bank of Irtysh). Farther, it goes along the border of the more or less high trunked forest, i.e. along the northern foothills of the Altai, and, enveloping this montane country in an arc, surrounds the Kuznetsk Alatau from the west and north, going on to Tomsk and thence to Novosibirsk. Spreading over the Barabinsk steppe from the north and proceeding slightly to the north of Lake Chana, the border of the range crosses the Irtysh a little south of 56° N. Lat., and the Ishim—somewhat

north of this degree, going on to Tyumen' and approaching the Ural range, covering Sverdlovsk region a little north and west (45–50 km) of the city. Along Urals, the range of the bear descends to the south as a large cape, reaching to 52° N. Lat., in the east including the sources of the Ural [river]¹³. Thus, in western Siberia, the contemporary range of the bear already does not occupy the steppe and the forest-steppe, and its southern border proceeds along the southern part of the forest (taiga) zone. In some sections of Siberia, for example in Cis-Baikaliya, in some places inside the range considerable areas have formed where the bear had been a comparatively short time earlier a common species, but has completely or almost completely disappeared. This was, unfortunately, favored by the attitude toward the bear as a predator, the hunting of which was in no way restricted.

- 419 In the European part of the Union, the natural range of the bear in the south occupied not only the entire southern part of the modern forest zone, but also the forest-steppe belt and was spread far within the limits of the modern steppe¹⁴.

Between the Volga and Ural, the animals lived along the Kinel', Samara, and in Zhiguli. The southern border, however, lay to the south. Passing from the Ural river (Ural'sk), it apparently included Obshchii Syrt and its southern spurs, extended to the Irgiz, and along it to the Volga. Thus, in this area, animals were also sufficiently widely distributed in the steppe zone. In some places, bears apparently moved farther to the south than has been stated.

The distribution of the animal in the Volga valley is not clear,

¹³ Border of range from Tarbagatai to the Urals according to Ognev, 1931; Shvarts, Pavlinin and Danilov, 1951; Kirikov, 1952, 1959; Yakushevich and Blagoveshchenskii, 1952; Sludskii, 1953; I.P. Laptev, 1958; Afanas'ev, 1960 and other sources.

¹⁴ In ancient times, our southern steppes were much richer in forests than in later times. The southern limit of forests from the Carpathians and Moldavia passed, apparently, approximately along 48° N. Lat., through the upper Ingul, Dnepr, the upper Berda and Mius to the lower Donets. To a considerable degree, these regions were bottom-land forests. Along the Dnepr, the bottom-land in the form of quite considerable massifs reached even to its mouth, and the same thing took place along the Bug and along other southern rivers. Considerable woody vegetation existed along the Don and its tributaries. The bear is ecologically very flexible and could have existed not only in the presence of entirely insignificant forest vegetation as in Kazakhstan, but also along the bottom-land forests, in shrublands along the river valleys, and even in the steppe.

but probably they extended along the bottom-lands quite far to the south since they were, apparently, quite widely distributed in the forest-steppe and steppe zone in the Don basin. Here, the animals lived along the entire Medveditsa to its mouth, and along its tributaries the Ters, Knyazevk, Karamysh, Idolga and Kamyshlei. Along the Don itself, bears lived not only in the north (Shipov forest around Pavlovsk) but also considerably lower—to Starogrigor'evsk station, at the mouths of the Khopr and Medveditsa, and even in the Kletskaya region. Along the Donets, bears lived mainly in the north—at Chuguev, Zmiev and in other places to the south, southeast and southwest of Khar'kov, but even in the region of the Oskol mouth, and they reached the location of present-day Lugansk.

To the west, the animals were distributed in Chernigov and Kiev districts and near Poltava. More accurate distribution of the animal along the left bank of the Dnepr is not known; however, it apparently descended to the south considerably beyond Poltava. It may be assumed that the border of the range went from the Donets to the Dnepr approximately at Zaporozh'e. To the south on the right bank of the Dnepr, there is some information concerning the occurrence of bears in Chermyi forest near Kirovograd, in the Savransk steppe southeast of Balta at the mouth of the Samotkan' river, and even in the steppes around Ochakov, on the lower Dnepr and at Perekop, i.e. bears were distributed to the shore of the Black Sea.¹⁵

Therefore, in the European part of the Union, bears were distributed not only in the forest-steppe but were widely encountered in the steppe zone, in particular, apparently, in its western part.¹⁶

In the west, the range of the bear in the past extended to the Baltic Sea and to the southwestern foot of the Carpathians—to the Pannonian plain.

Information concerning Ural'sk, Volga, Don basin and Chernyi forest is from the 18th century; data about Balta, lower Dnepr, Ochakov and Perekop, to the 16th–17th [centuries]. Fossil remains of bears from the Pleistocene are known from the Crimea.

¹⁵Border of range in European part of Union according to Kirikov, 1952, 1955, 1959; in part Korneev, 1952; Sokur, 1960 and other sources.

¹⁶Ochakov bears were even called by the author who described them (Bronevskii) "steppe bears" "*Ursi campestris*" (cited from Kirikov, 1952). In this respect, our southern bears (as in Kazakhstan) are entirely analogous to some American forms.

The described reconstructed southern limit of the range of bears in the European part of the Union, in contrast to the northern, has been very strongly changed during the last century, and displaced northward for hundreds of kilometers—in places almost 1000 kilometers and perhaps more. An entirely intensive process of range reduction has gone on in the 20th century, particularly in the last ten years. The border did not change so quickly during the entire [previous] history of the species. Not only the deficiency in the accurate data, but also to a less degree, the stated situation does not make it possible to give the contemporary southern border of the range with sufficient accuracy—it changes before the eyes from year to year. It has changed more and, apparently, more quickly, than the southern limit in Siberia.

In the 40's and 50's of our century (until 1960), the southern limit of distribution of the bear in the Ural [mountains] and the European part of the country might be outlined as follows. Starting at the eastern slope of the Ural, approximately 50 km west of Sverdlovsk, it passes directly southward along the eastern edge of the Ural forests, occupying the range (Shaitantau) south of approximately 52° N. Lat. Thence, the border turns sharply northward, defining a Ural "extension" of the range on the west. The border goes along the foothills west of the Ural without crossing the Beluya [river]. Somewhere in the vicinity of 60° N. Lat. it curves sharply to the west, dividing the northeastern part of Perm district, where bears still exist, from the remainder, in which the animal is already extinct. The westward trend of the border quickly changes to the southwest and then to western again—the border, descending to the lower Kama, bypasses it from the north and crosses the lower reaches of Vyatka, thus encircling Tatar Republic from the north. Here the bear, as a permanent inhabitant, was already absent at the end of the 20's—start of the 30's, although individual transgressions moving down from the northwest (from the Marii ASSR) still occurred locally in the 40's, 50's, and even 60s. Migrating animals almost immediately fall prey [to hunters] (V.A. Popov).

Crossing the Volga, apparently somewhere in the vicinity of 48° E. Long., the border goes on steeply southward, extending over the forests of Sura basin and descending here quite far to the south, approximately to 54° N. Lat. Thence, turning somewhat northward, the border proceeds along the level of Temnikov in the Mordovsk Republic, westwards to the Moksha, and through the forests of the

Tsna basin, producing a long, very narrow, extension southward. However, this extension does not reach Tambov. These data belong to the past decades; however in 1960, the bear was already absent throughout the forests of Tsna and Moksha except the Sarovsk forests (Zametchinskii region, K.I. Nagornov).

From the region around the mouth of the Moksha, the border proceeds somewhere along the left bank of the Oka [river] at a distance from it, then suddenly descends southward, making a loop which includes Ryazansk Meshchera. The southern border of this loop passes along the Pra river. From the Pra, the border turns abruptly northward, and passing first through the regions of Vladimir district, surrounds the Moscow [district] from the east, north and west.

In the Moscow district, bears even a short time ago were quite widely distributed and lived not far from Moscow. In 1891, a bear started from a wolf's den was killed at Pushkin (about 30 km from Moscow along the Northern railway). Even in the 20's, the animals lived regularly in the former Bogorodsk (Noginsk), Dimitrovsk and Klinsk counties (the east, northeast and north of the district). In the 20's, they were still found in the then Dolgolugovsk forest plantation, which included the vast forests around Khot'kov, Sofrin and Pushkin (along the Northern railway—between Moscow and Zagorsk); they also existed in the forests around Zagorsk and farther north. The bear began to disappear quickly in the 30's, and in the 40's and 50's, was no longer in the nature of a permanent inhabitant of this region; it very rarely appeared as a transient moving from the north along the Dubna or from Meshchera to the forests around Shatura, i.e. from the east and southeast (Ognev, 1931; Formozov, 1947; V.G. Heptner). The last of such transients occurred locally on 7 December 1960 in the exceptionally warm winter, when a *shatun** was killed in the forests at Lukhovits (newspaper "Vechernyaya Moskva", 24 December 1960).

A somewhat exact location of the border in the Ivanovsk, Yaroslavsk and Kalininsk district is impossible. Apparently, the range includes the western parts of Orlovsk district and, perhaps, Kaluga district, since in the 50's it included all of Bryansk district except
421 its extreme southern parts (Brasovsk, Sevsk, Novozybkovsk,

*Starving, non-hibernating bear in winter; see p. 676—Sci. Ed.

Klimovsk, Klintsovsk and Starodubsk *leskhoz* [forest cooperatives]; (Fedosov and Nikitin, 1951).*

In Vladimir district the bear was already absent in the 50's (N.D. Sysoev).

In Byelorussia, where the bear was, a short time ago, widely distributed almost everywhere, in 1950–1951 it was already found only in the northern regions. The border passed farther north of Mogilev and northeast of Minsk, but then turns sharply to the northwest and north, and passes through the regions of Borisov, Pleshchentis, Begoml', Donshchitsa, Glubokov and Markovshchina. A small center of occurrence of the animal, separated from the Northern Byelorussian, is found in Belovezhsk Forest (Serzhanin, 1955). Farther to the north the limit occupies, apparently, the western extreme of Latvia (in Lithuania, the bear is now absent), going into Estonia. Here, in 1976, the bear was quite widely distributed, being encountered west of a line from Pyarnu (Riga Gulf)—Cape Yumind (Gulf of Finland), and in the north reaching to the Gulf of Finland and in the south to 58° N. Lat. A separate section of occurrence, which a short time ago was still connected with the main part, is found northeast of Khapsala (Kh.I. Ling).

From northern Estonia, not so far from the coast of the Gulf of Finland, the boundary passes eastwards to Leningrad. In the west of Leningrad district, the range enters the regions of Luga, Slantsev and Kingissen. Bypassing Leningrad to the south and east, the border passes through Gatchina (about 40 km from Leningrad), Vyritsa (60 km), Tosno (about 60 km), Lisino (45–50 km, along the highway to Moscow) and Mga (about 40 km; N.K. Vereshchagin), and goes on to the shore of Lake Ladoga and, surrounding it, passes into Karelia. On the Karelian isthmus, the animal is absent. The state boundary constitutes the western border of the range in Karelia and farther north.

Inside the region defined by the above mentioned line of the southern boundary, the distribution of the animal is very uneven and, equally with regions where the population is found in a more or less normal condition, there are considerable expanses where it is reduced (western and eastern parts of Leningrad district), or the animals are very rare or appear only as transients. In considerable

*No initial parenthesis in Russian original—Sci. Ed.

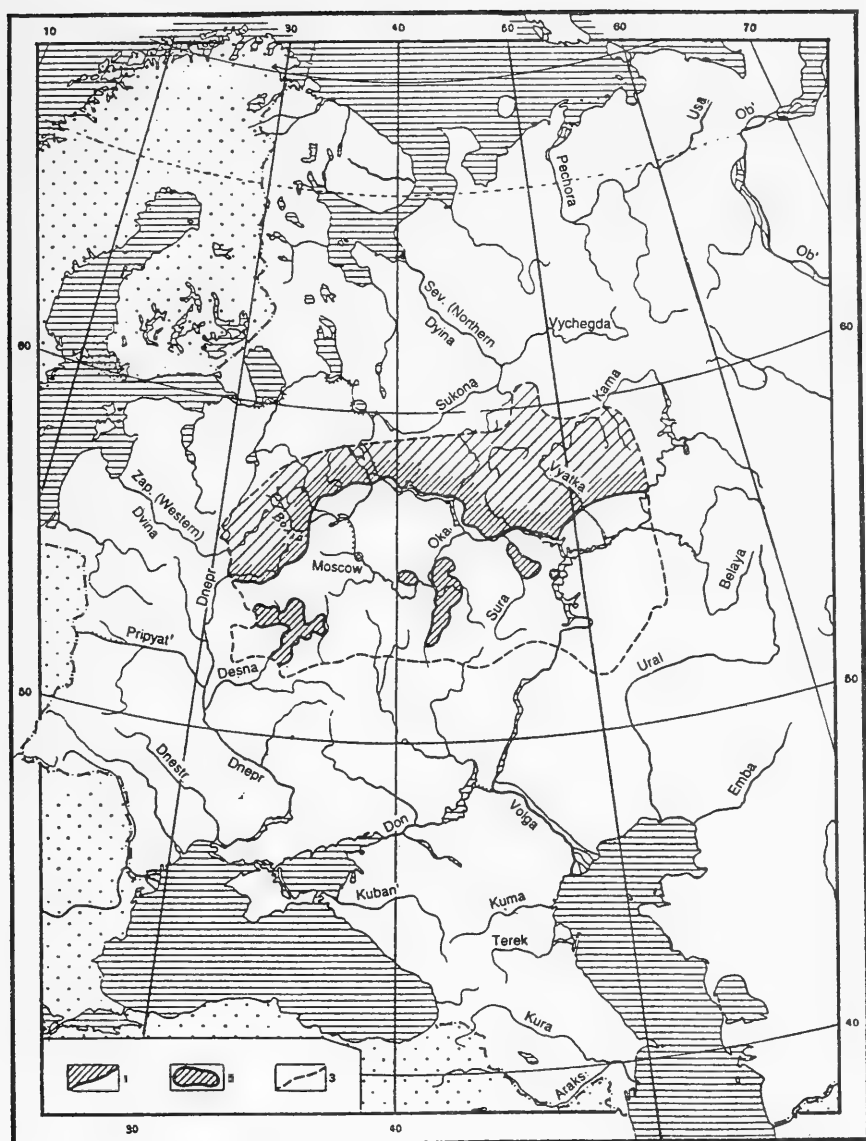
areas inside the range the bear is already completely absent. It is impossible to characterize various parts of the range in this respect, not only because of the absence of information in the literature, but also because the distribution and numbers of bears changes very quickly in a negative direction—literally in individual years. Thus, if in the beginning of the century the bear was common at any place in the northern districts of the Ukraine, by the end of the forties, only individual transient animals from Byelorussia to the northern parts of Chernigov, Zhitomirsk and Volynsk districts were met with, and later, they completely disappeared. In Byelorussia a short time ago, the animal was distributed almost everywhere, while at the present time, its range is restricted to the above-described northern part, and so on.

The picture which is shown of changes in distribution and, in part, numbers of bears at the southern limit of the contemporary range, are indicated by special investigations carried out in 24 middle districts in 1962. These districts lie from the upper Dnepr in the west (boundary of Byelorussia) to the Kama in the east. Within this territory, the bear inhabits only forest massifs of large area, therefore the southern limit of its distribution coincides quite exactly with the recent limit of large expanses of forest. In Smolensk district, the border passes along the right bank of the Dnepr, and in the neighborhood of Dorogobuzh, a small amount of bears are encountered in forests on the left bank of the Dnepr, which are rich in swamps. From Dorogobuzh, the boundary ascends north-northeast as far as the village of Sychevka, whence it passes along the left bank of Volga to Kalinin and beyond to Bezhetsk and eastward to Uglich and Tutaev. Farther on, the boundary again goes long the right bank of the Volga to Zelenodol'sk (Tatariya), thence ascends northeast towards to Malmyzh, Vyatskie Polyana and Izhevsk.

423 North of this line during the time indicated, the bear is met with everywhere; however, to the south, there were only a few separate sections of its occurrence:

1. the forest massif between the cities of Kostyukevichi, Kletnya and Roslavl' within Bryansk and Smolensk districts (up to 10–15 individuals);

2. the forest massif along the left bank of Desna, in the interfluvium between the Zhizdr and Rasset rivers, and the sources of Vytebet' river within Bryansk, Kaluga and Orlov districts (from 20 to 30 animals);



422 Fig. 153. Details of the distribution of the brown bear *Ursus* (*Ursus*) *arctos* L. in 24 districts of Middle Russia (outlined by dashed line—3) from the upper Dnepr (eastern boundary of Byelorussia) to the Kama. In the north (1) district of more or less general occurrence. Outlined separate sections (2) farther south of the general boundary—individual isolated areas of occurrence, separated from the general range in the north. Data for 1962 (V.P. Teplov and S.G. Priklonskii).

3. Meshchera forest massif along the left bank of the Oka in Ryazan district (5–10 animals);

4. the forest massif along the banks of the Tsna, middle course of the Moksha and right bank of the Oka within Tambovsk, Penzen, Ryazan, and Gor'ki districts and Mordovian Republic (30–40 bears);

5. the forest massif along the right bank of the Sura in the Chuvash Republic (15–20 animals);

6. the forest on the right bank of Kuibyshev reservoir south of the city of Tetyusha (in 1960, a female with cub) [Fig. 153].¹⁷

In the sixties, a transient bear was recorded in Taldomsk region of Moscow district and near Vyazniki of Vladimir district (V.P. Teplov and S.G. Priklonskii).

In 1960, as a remnant of their [once] wider range in the European part of the Union, there is quite large, entirely isolated area of bear habitat within our country in the Carpathians. It consists of a small belt extending in a northwestern direction from the Romanian border (from a place southwest of Chernovtsy) and nearly to the state boundary with Poland, south of Drobych. It is a region of taller, denser Carpathian forests within Zakarpatsk [Trans-Carpathia], Chernovitssk and L'vov districts. In particular, the range includes Chernogor Gorgan, Beskid and Borzhavsk *polonina** and other parts. This section represents a continuation of the range of the bear in Romania.¹⁸

The Caucasian section of the range in our country was, apparently, not connected with the European-Siberian part during the historical period. The connection was affected through Central Europe, the Balkans and Asia Minor. However, in the Holocene the northern population of bears was connected with the Caucasian through the steppe region. Bears undoubtedly lived along the bottom-lands of the southern Russian rivers and the rivers of the northwestern Cis-Caucasus, and in steppe ravines and reeds of this region. In the lower Don, the animals were encountered even in the

¹⁷ Information concerning occurrence of bears in Tatariya, except as previously mentioned, is considered unreliable (V.A. Popov).

* Local word for montane meadow—Sci. Ed.

¹⁸ Described southern limit according to Ognev, 1931; Popov and Lukin, 1949; Heptner, Morozova and Tsalkin, 1950; Kuklin, 1951; Fedosov and Nikitin, 1951; Shvarts, Pavlinin and Danilov, 1951; Kirikov, 1952, 1959; Korneev, 1953; Serzhanin, 1955; Tatarinov, 1955; Savinov and Lobanov, 1958; Sokur, 1960 and other sources and materials of N.K. Vereshchagin and V.G. Heptner.

8th–13th c[enturies]. The former direct connection between Caucasian and Russian bears is shown by several peculiarities of geographic variation of bears of the Caucasus (see below).

In the past, the range covered all of the forest regions of the country; i.e., in the main, the entire Caucasus—Great and Lesser, as well as the western Trans-Caucasus from great heights to sea level.¹⁹ The animal was absent only in the steppe region of the eastern Trans-Caucasus, although they penetrated along the *tugai* forests of the Kura into forestless districts at least to the level of Alazan'; perhaps they were also found along some other rivers. It is possible that the bear was absent in some forestless desert places in the
425 mountains of inner Dagestan, in the desert expanses of the Erevan depression and, perhaps, in several other relatively small sections.

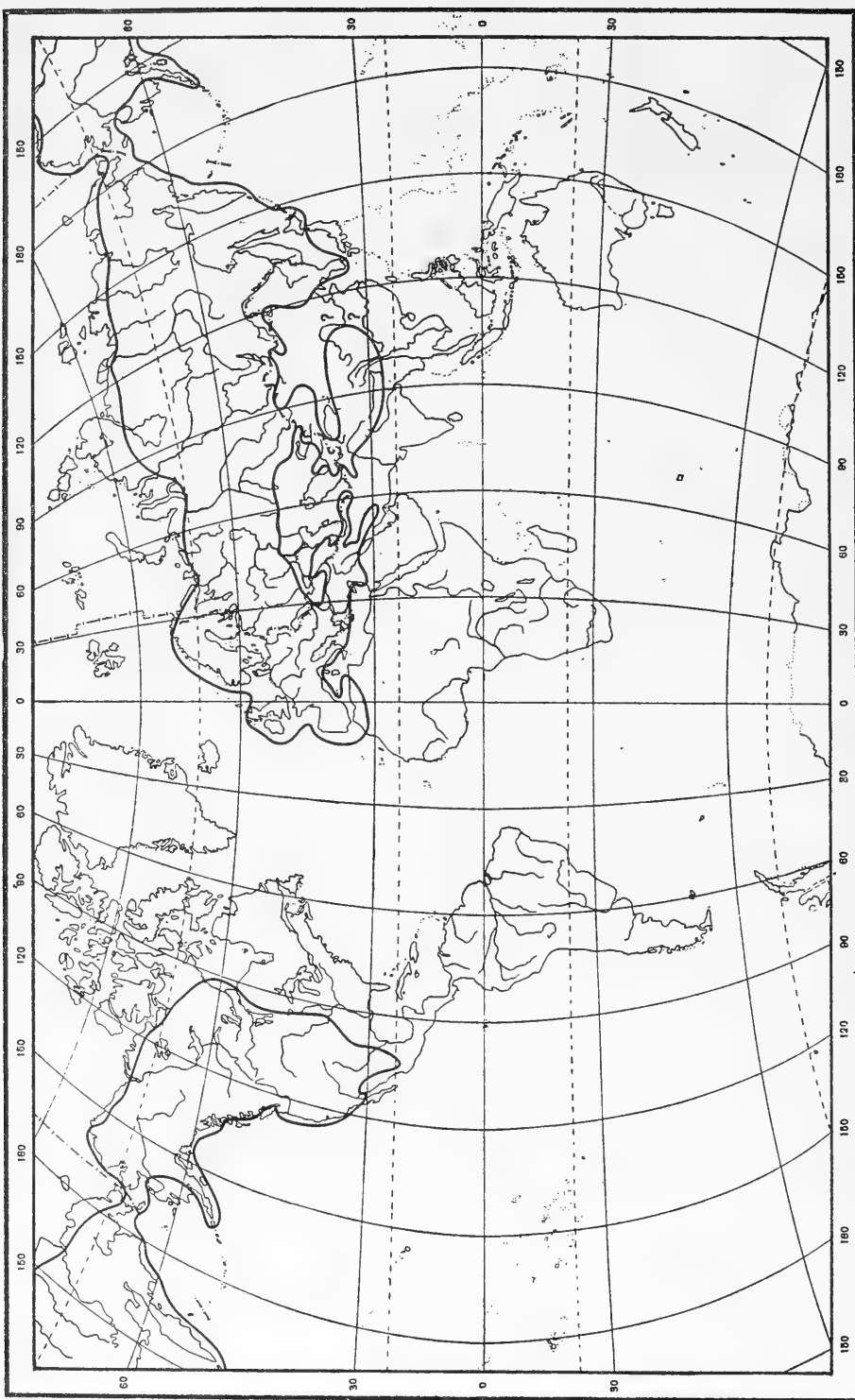
Along the Glavnyi [Main] Caucasian range, the range began at Anapa in the west, and in the east reached the shore of the Caspian [Sea]—to the forests in the foothills of Dagestan and the forests along the lower Samur river and mouth. It occupied the entire forest of the northern premontane and foothill area as far as Maikop, Pyatigor' (Zheleznovodsk), Nal'chik, Ordzhonikidze (Vladikavkaz) and Khasav'yurt. The forested areas of the Stavropol' uplands were even included in its range.²⁰

At the present time, the range of the bear in Caucasus has been reduced, in some place considerably. In part this even took place in the past century, and in part, even mainly, in our century—in the second quarter of it. The bear is absent in Pyatigor'e (here it only rarely intrudes), stretching the border, in part in connection with great clearings, from the northern foothills; the bear is now absent at Maikop, it has nearly disappeared from Kabarda and Balkariya, at Khasav'yurt, etc. The animal has disappeared from many regions of the western Trans-Caucasus (Kolkhida); the region of its occurrence in Armenia has somewhat decreased. The bear is nowhere present in the steppes of the Trans-Caucasus, it is almost never encountered in Talysh, etc.

In the Trans-Caucasian steppes at Stavropol', it disappeared more than 100 years ago; along the Black Sea coast, the bears still

¹⁹Bears are able to live in nearly forestless mountains, transgressing to entirely forestless desert mountains, and, in summer, are found everywhere in high-montane (alpine) meadows.

²⁰However, Dinnik denies the presence of bear in "Stavropol' governance".



424 Fig. 154. Reconstructed species range of the brown bear, *Ursus (Ursus) arctos* L. Question marks refer to regions of possible occurrence in the distant past. Places of individual transgressions are not indicated (V.G. Heptner).

occurred nearly to the sea, even in our day; at Khasav'yurt it lived in the 90's [1890's] and 10's [1910's]. In the beginning of the 20's, it was found in the forests of the foothills ("Chernye Gory") actually only some kilometers from Ordzhonikidz (Vladikavkaz). Almost everywhere, especially in the Lesser Caucasus, the number of animals has been reduced.²¹ Accurate data on the recent distribution of the bear in the Caucasus are very few. Generally, its range is connected with its direct pursuit, and with its reduction as forests steadily decrease.

In Middle Asia, the range of the bear is associated with mountains, such that the bear here lives in some places where there is only a sparse growth of woody junipers or pistachios, or shrubs in ravines; in some places, it exists in the entirely treeless, even desert mountains.

The reconstructed range in Middle Asia and Semirech'e occupies the Saur, Tarabagatai, Dzhungarsk Alatau and the whole of the Tien Shan system including the western ranges and Karatau. Furthermore, its distribution includes all the ranges of Pamir-Alai system westward to the western parts of the Turkestan, Gissar (V.G. Heptner; Leviev, 1939) and Darvazsk ranges. In Kugitangtau and Babatag, and in some other elevated interfluves between the right tributaries of the Amu-Dar'ya, the bear was absent from time immemorial, or at the very least for a long time. Apparently, the range did not include the Nuratinsk mountains. In Turkmeniya, the range occupied the Kopet-Dag; however, in Great Balkhan, in the mountains on the right bank of the upper Tedzhen (Gyaz'-Gyadyk), and in the mountains east of Kushka (Chengurek mountains), the bear was absent (V.G. Heptner).

It is impossible to clarify the recent range of the bear in Middle Asia in more detail due to insufficiency of information. As compared to the above-described, it undoubtedly changed during the past century and particularly during the last ten years—the general area of the range decreased, and significant "gaps" appeared in it, but apparently the animal is still encountered in the majority of the mountain ranges where it previously existed. However, it is now

²¹Distribution of the bear in the Caucasus according to Dinnik, 1914; Satunin, 1915; Smirnov, 1916, Ognev, 1931; Heptner and Formozov, 1941; Vereshchagin, 1947, 1959; Dal', 1954; Tembotov, 1960, and other references, and according to materials of V.G. Heptner.

absent in Karatau, and disappeared, or is only met with very rarely as a transient from Iran, in the Kopet-Dag (V.G. Heptner).

Geographic Range outside the Soviet Union

426 In Asia, the reconstructed range occupies the islands of Hokkaido, the Korean peninsula and northeastern China, except its central steppe areas; i.e. mainly the mountains of the Great Khingan, Il'khuri-Alin', Lesser Khingan, the eastern Manchurian montane region, Chanbaishan', Kentei-Alin', Laoelin and Chzhanguantsalin. In the Mongolian Republic, its distribution occupies, in the north, the Khentei ranges and the Cis-Hobsogol part of the country southwards approximately to 48°30' N. Lat., at the boundary with the USSR along the left bank of the Selenga river. In China, in the extreme west, the range occupies the eastern part of the Tien Shan region, in Kashgariya and Dzhungariya, in particular the Borokhoro mountains at Barkul'. Thence, the range extends as far as the Trans-Altai Gobi, the Gobi Altai, and the southeastern part of the Mongolian Altai in the M[ongolian] P[eople's] R[epublic].*

Farther, the range includes all of Tibet, including Nan Shan, and Tsaidam, the region south of the great bend of the Huang he (Tsing-ling mountains northward) and, apparently, northern and western Sichuan. The question of the occurrence of bears in the eastern part of China to the east of the described limits remains open. It is not excluded that bear never existed there; however, civilization has eliminated all natural relationships in this region so that this cannot be clarified.

To the south, the Central Asian region of bear occurrence covers the Himalayas, including Nepal, Kumaon, Kashmir with the Karakorum and northern Punjab, and Waziristan. This animal as described does not, apparently, penetrate further to the south (into Baluchistan). In the east, the animal does not get into Burma (information concerning its occurrence in the Shan region is unverified).

In Afghanistan, the range occupies the regions associated with the Pamir (Badakhshan, Wakhan), and the Hindu Kush. Details are not known. In Iran, the range occupies on the one hand the extreme northern region—forested districts associated with [Mt.] Elburz—and extends as a band from the Talysh to Kopet-Dag. On

*Isolated population also in extreme southern Gobi desert, along border with China—Sci. Ed.

the other hand, it proceeds as a wide projection from northern Iran to the southeast along the western and southwestern part of the country through Luristan approximately to Shiraz. In central, southern and eastern Iran, the described species is absent. The range occupies all of Asia Minor (montane sections), and montane districts of northern and western Syria, Lebanon and Palestine.

In Europe, beyond our borders, the reconstructed range occupies substantially all of the continent to the extreme north, including, in the west, England and Ireland; southwards, it reaches to the shores of the Mediterranean Sea including the Apennine and Pyrenees peninsulas. In Sicily, Corsica and Sardinia, the bear was absent as well as on the islands of the eastern part of the Sea.

In Africa, the bear occupied the Atlas mountains.

In North America, the range of the brown bear (reconstructed) occupies the western half of the continent, approximately west of 90° W. Long. The southern limits of the range, starting along the shore of the Pacific Ocean, include the northern part of the [Baja] California peninsula. On the continent, continuing at some distance from shore of the Gulf of California, it descends along the Mexican plateau to the southern part of the province [state] of Durango, approximately at 20° N. Lat. This is the southernmost point of occurrence of the animal in the New World. Thence, the border outlining this southern extension on the east goes northward through northeastern Mexico (Coahuila) into Texas (USA), leaving its western part within the range boundary. Extending farther in a northern direction, the boundary leaves within the range Oklahoma to the west and the greater part of Kansas, and goes directly northward through the western edge of Iowa and Minnesota and through the eastern part of Manitoba, passing to the shore of the Hudson Bay at Churchill. Running farther north along the western shore of the Bay, the boundary turns to the northwest somewhere around Chesterfeld Inlet and reaches the northern coast of the continent. Along it, and in places some distance from it, the boundary proceeds westward, transecting the shore of the Bering Sea and covering the Alaska Peninsula and Kodiak Island, continues along the coast of the Pacific Ocean southward to the previously described locality in California. Not included in the range, apparently, is that western part of the territory lying to the north of Bristol Bay in which are found the lower Yukon and Kuskokwim [rivers]. The brown bear is known from St. Lawrence Island and Unimak in the

Bering Sea; on others it is absent. Brown bears are absent also, apparently, on the Queen Charlotte Islands and Vancouver Island.

The recent range of the brown bear differs very strongly from that as outlined, and comprises only the smaller part of it. At the same time, the range has been divided into separate, comparatively small, sections—often very small—which are entirely separated from one other. In the whole of the range as outlined, there remain only some more or less big areas inhabited by the animal. The largest of these is the European-Siberian area within the USSR; the Central Asian is quite large; and a considerable area exists in North America.

In Europe at the present time, bears remain in Norway, Sweden, and Finland; in the French and Spanish Pyrenees; in the Cantabrian mountains in Spain; in the Italian Alps, the middle part of the Apennines; in Poland, Czechoslovakia, Hungary, Romania, Bulgaria, Albania and the European part of Turkey. They are most common in Scandinavia, in parts of Bulgaria and Yugoslavia, and especially in Romania. In the other countries mentioned, the animals are very scarce and in part are found only as individual specimens. In Africa, the bear became completely extinct long ago.

In Asia, outside the borders of our country the bear has been conserved only in Asia Minor (in places), northern Iraq and in the above mentioned part of Iran. In Japan, it has been exterminated. The range on the Korean peninsula and in the Mongolian Republic has decreased and continues to decrease. That part of the range occupying Tibet and adjoining places in the Himalayas, is still large.

427 In America, the range has decreased very greatly. The animal is still widely distributed in Alaska, in northern and western Canada (except Manitoba), but in the United States, it is substantially, found only in the Rocky Mountains in the states of Montana, Idaho, Wyoming and Colorado. An isolated section of habitation is found far to the south on the Mexican plateau.²² It is evident that farther reduction in range and numbers of the animal is inevitable (V.H.).

Geographic Variation

Geographic variation in bears has always attracted attention, especially in the first half of our century. At the same time, many

²²Recent distribution of bear in Europe and America according to Couturier (1954).

errors and misrepresentations have been made in its study such as, so it seems, have not been made in the investigation of variation of any other species of carnivorous mammals. Bears were the object to which was applied a unique concept of Merriam's (1918), who accepted 77 "species" and 9 races for only the North American part of the range, the majority of which he himself described. This astonishing scheme is at present encountered in the American literature (Miller and Kellog, 1955).²³ A special genus of brown bears was even described. This applies not only to the American forms, where the misrepresentations are especially great, but also to animals of the Old World, including those living with us. The situation noted, if one sets aside simple lack of ability and knowledge, is explained partly by the undirected theoretical positions of some authors and by the lack of study of the species question in the recent past.

The large nongeographic variation in the bear (see above) creates essential objective difficulties. Particularly in this respect, individual differences are important. In some places (Caucasus) dark and light, large and small animals of the same age may live side to side. The existence of animals of different dimensions in one place is especially remarkable.

Individual differences in the skull are especially great—not only in dimensions, but also in protuberances, crests, etc. profile, general massiveness and others. The degree of tooth wear may be very different in animals of the same age, which may perhaps be associated with characteristics of foods of animals in various localities, etc. Lastly, intensity of hunting may affect general dimensions of the animals, and belonging to a definite population, as well as their cranial characteristics. In one locality, the animals may live to greater age and size than in another, and these differences may appear to be entirely real systematic ones. It is quite natural that with a small collection of material and a mainly morphological concept of species and races, there was formed an exaggerated representation of geographic variation in our bears (Smirnov, 1916). For our territory, Ognev (1936) even accepted 6 species of bear, as well as one of

²³Only in the most recent time has the species unity of the North American brown bears been clearly stated (Rausch, 1962) and interesting data were presented concerning the clinal type of variation in several important characters (condylobasal length, i.e., general dimensions).

them with 8 races. This arrangement was held for a long time, although even in the middle 30's, more sensible opinions were expressed about geographic variation of bears.

In general the trends in the Old World in geographic variation in bears and their corresponding races can be traced in several main directions.

1. European-Siberian bears (group *arctos*). Size moderate, in places small, dark color type predominates, light type relatively rare. Claws dark.

428 Europe, Caucasus, Siberia except the east, northern part of the M[ongolian] P[eople's] R[epublic].²⁴

2. Near Eastern bears (group *syriacus*). Size moderate and small. Light color type predominates, dark is rarely encountered. Claws light or near-light.

Part of Trans-Caucasus, Palestine, Lebanon, Syria, Iraq, Asia Minor, Iran, Afghanistan, western Himalayas, Pamir-Alai and Tien Shan mountains.

3. Far Eastern bears (group *piscator*). Size large and very large. Dark and very dark colors predominate, light color type is also met with but more rarely than in European-Siberian bears. Claws dark.

Far East and in part eastern Siberia from our southeastern border to Kamchatka and extreme northeastern Siberia.

4. Tibetan bears (group *pruinus*). Size moderate. Fur is particularly long and shaggy; light and dark color types are encountered approximately equally (intermediate color predominates). Often lighter on the neck ("collar"). Claws light. Skull distinguished by relatively flattened choanae (internal nares), arch-like curve of molar row, larger teeth and several other characteristics.

Tibet and several contiguous countries.

The Tibetan bear group differs from other groups more than they differ from each other, and many authors considered this group as an independent species (Flerov, 1935; Allen, 1938). For this there is, apparently, not sufficient foundation, although the Tibetan group, to a certain sense, may be contrasted with all others.

²⁴The question concerning the North African *U. a. crowtheri* is set to one side. This is a "mythical animal" (Harper, 1945) which became extinct more than 100 years ago, of which no specimens are preserved in museums.

Within the boundaries of our country, all of the racial groups are represented, except the Tibetan. The relationship of Tien Shan bears to them (to "species" *pruinus*) is without foundation.

It is difficult to form an opinion about the groups of races existing in America for the reasons given above. Apparently, there are two main ones: 1) a group of large and very large bears of northwestern Alaska and the coastal regions of the Pacific Ocean southward to Dixon Strait [Entrance] (about 50° N. Lat.), including Kodiak Island (forms *beringianus*, *middendorffii*, *gyas* and several others); and 2) races of the "grizzly" group occupying all remaining part of the species range in America (Haltenorth and Trense, 1956). The first group is, undoubtedly, the same as the Far Eastern one of the Old World (group *piscator*); the second is, apparently, analogous (parallel) to the European-Siberian (group *arctos*) and Near Eastern (group *syriacus*). There is obviously no sharply delineated group such as the Tibetan (*pruinus*) in the New World.

After Ognev (1931) had published his unsuccessful scheme of geographic variation in bears, this question was dealt with by many authors as regards bears of the Old World. Only few of them (Adlerberg, 1935; 1935a; Flerov, 1935) used good collections and were able to contribute something substantive. The majority of them (see review by Couturier, 1954) did not have sufficient material from our country and combined data from literature. Their review contributed little of use and sometimes confused the picture even more. There is not yet a true contemporary analysis of geographic variation. The data given below are preliminary and only note more well-defined subspecies.²⁵

European-Siberian bears—group arctos

1. Middle Russian bear. *Ursus (Ursus) arctos arctos* Linnaeus, 1758 (synonyms, all the above mentioned synonyms, except those mentioned below for other races).

²⁵Couturier's opinion (1954), wholly denying the existence of subspecies of brown bear is only "a gesture of despair" and of course, cannot be accepted. The presence of real races is not in doubt, and the question lies only in their number, in the evaluation of populations with intermediate characters ("transitional"), in nomenclature, and so on. While denying the presence of subspecies in bear, Couturier accepts, however, the occurrence of numerous separate "populations", which, of course, does not help in clarifying the picture.

Size moderate.²⁶ Pelage of moderate length, density and softness. Color varies from very dark blackish-brown with rusty-gray highlights, depending on lighter terminal parts of guard hairs, to light straw-brown with translucent dark-reddish-brown underfur. Underfur is always dark. Limbs are darker than body; in light forms, muzzle is darker than trunk, dark spot (area) on withers absent. Collar is sometimes developed, but is narrow, not covering entire base of neck, or not developed on nape. Occasional individuals of extreme color are almost black with a weak admixture of brown tone, or almost straw-yellow.

Details of coloration of the two main types are as follows. Light type: general tone is brownish-straw with translucent dark underfur. Base of guard hairs and underwool red-brown, dark. Muzzle brownish-rusty. Lower lip and chin darker. Forehead and side of head gradually lightening, imperceptibly grading into light color of neck and trunk. Ears dark, same tone as lower lip, hairs on them [ears] lacking light tips. Hairs on neck and trunk dark, red-brown, guard hairs have broad (about 2 cm) light tips. Tail dark brown, without light highlights. Limbs dark brown, without admixture of light hairs, quite sharply delineated from the lighter trunk. Claws are dark horn or blackish-brown color.

Dark type: general tone blackish-brown, sometimes with weak light highlights (gray hair). Base of guard hairs brownish-black, underwool brown. Muzzle dark, chestnut brown. Forehead and side of head gradually lightens posteriorly. Ears dark brown without light tips on guard hairs. Trunk and neck have guard hairs with very short light tips. Belly and limbs are very dark, brownish-black. Claws as in light type (Flerov, 1935).

Both types are connected with each other by a full series of transitions, the dark type predominating ("brown" according to furriers), especially in the western part of the range (in the middle districts of the European section of the country and to its north, bears are dark).

Greatest length of skull in males,²⁷ 311–M 325–388 mm, females—279–M 301–336 mm; condylobasal length of skull in males,

²⁶Characteristics here and below employ data of Ognev, 1931; Flerov, 1935; and Kuznetsov, 1952, with some changes and additions.

²⁷Measurements here and below based on data of Ognev (1931).

300–M 320–343 mm, females—269–M 286–313 mm; zygomatic width of skull in males, 117–M 207–231 mm, females—147–M 174–192 mm; length of upper tooth row in males and females—106–M 117–125 mm.

Maximum weight 320–350 kg, as a rare exception, larger. Animals of the European part of the country are now smaller than West Siberian, which is explained mainly by intensity of hunting in the west. In the past century, this difference was less and very large bears were encountered around Moscow.

European part of the Union, Urals, West Siberia approximately to the Yenisei [river], and Altai (?).

Outside the USSR—Europe.

The eastern distributional border of this form is not established and, apparently, is very indefinite. There is information that animals of this race are distributed eastward, especially in northern Siberia, farther than mentioned here.

2. East Siberian bear, *Ursus (Ursus) arctos yeniseensis* Ognev, 1924 (synonyms *baicalensis*, *kolymensis*; to this form the name *collaris* is also given).

430 Dimensions larger than in Middle Russian bear (*U. a. arctos*), but generally, considerably less than those in Far Eastern subspecies. Particularly large individuals, however, often attain dimensions characteristic of the latter. As with the latter, there are forms corresponding to *U. a. arctos* or slightly exceeding it in size.²⁸ On the whole, the range of individual variation in general dimensions and skull measurements is very great—greater than that in *U. a. arctos* and, apparently, greater than in Far Eastern forms.

Pelage long, dense and soft. Coloration generally of same type as in Middle Russian form, *U. a. arctos*, but individuals of darker color predominate (by terminology of furriers, “dark brown”).

Greatest length of skull of male is 326–431 mm; condylobasal length of skull—312–385 mm; zygomatic width is 193–252 mm; length of upper toothrow is 121–143 mm.

East Siberia, beginning approximately at Yenisei [river], as far as Trans-Baikaliya, Stanovoi range, Lena and Kolyma basins, and generally throughout Yakutiya; Altai (?).

²⁸Namely these small bears were qualitatively described as special forms (*baicalensis*, *kolymensis*). This notwithstanding that within the limits of the broad range of these subspecies, there are small populations of the small bears.

Outside the USSR—northern part of Mongolian Republic. The described form has been, so far, insufficiently studied entirely.

Ognev (1931) accepted three subspecies for the territory outlined above, giving them completely contrasting characteristics. Adlerberg (1935) and Flerov (1935) assigned animals in the described territory to *U. a. arctos*. The same was done by several of our other authors, following them without special study of the question (Bobrinskii, 1944; Novikov, 1957).

The actual situation, apparently, is consistent with the view that the broadest part of Siberia is inhabited by a population occupying an intermediate position ("transitional") between European-Siberian *U. a. arctos* and the group of Far Eastern races. The picture of character distribution in the sense of their maintenance in populations and, in part, their distribution within the territory, is complicated. The normal type of bear here is larger than to the west, and extraordinary large animals are encountered which are not inferior, or only slightly inferior to typically large individuals of Far Eastern bears. These animals, in part very old, occur, moreover, not only in the east near the range of Far Eastern forms, but also in the west—in the Yenisei basin (particularly in its upper reaches), and along the Vilyui. Beside animals of this type, throughout the whole region individuals are met with, not differing in skull dimensions from *U. a. arctos*, or slightly differentiated from them. They even appear far to the east (in Anadyr territory; Ognev, 1931), coming together here with typical Far Eastern animals (*piscator*).

Altogether, this gives a picture of a transitional zone, where characters are related both with intraspecific hybridization, as well as, apparently, a gradient [cline] between them. The particular complexity of the picture is probably also caused by the presence of transition between not two, but three, races: the nominal with the two Far Eastern forms—the northern (*piscator*) and southern (*lasiotus*), which themselves introgress with one another (see below).

Assigning animals of the described region to the nominal form is, apparently, not any more, or only a little more, founded than assigning them to one or another Far Eastern [forms]. Since the range of bears of the above-mentioned type does not itself represent a narrow "transitional strip", but is very broad (all of eastern Siberia), there is a basis for recognizing them as separate subspe-

cies, perhaps of hybrid origin, and naming them. However, the uncertainty of morphological characteristics of the race makes the limits of the range distribution poorly defined, especially in the west.

431 The described form is analogous, in several respects, to the Caucasian bear *U. a. meridionalis* (see below).

Note: In contemporary foreign literature (Ellerman and Morrison-Scott, 1951; Haltennorth and Trenze, 1956) the form *U. a. collaris* Cuvier et Geoffroy, 1824 is frequently mentioned as Siberian. Pocock (1932) reestablished the forgotten and poorly defined name. The range of this form is given as "Siberia", in the upper Yenisei (Ellerman and Morrison-Scott, 1956 did not give its overall range). The forms *yeniseensis* and *sibiricus* are assigned it as synonyms. One of the main characteristics of the subspecies is designated as the well-developed light collar (Pocock, 1932). At the same time, in the upper Yenisei and in Siberia, there are no populations which could be characterized by a light collar, although there might be a more or less significant percentage of such individuals. Everywhere, this is a rare individual deviation. Moreover, the epithet *collaris* applies to it. Therefore, this character does not offer the possibility of establishing a type locality. Its indication as "Siberia" is too general. In Siberia, as it is usually understood by foreigners, there are three races in which a collar is occasionally found. In the beginning of the nineteenth century, "Siberia" most probably referred to western Siberia, i.e. the region of occurrence of *U. a. arctos*. The name *collaris* must, apparently, be considered a synonym, or must not, in general, be given any nomenclatural significance (*nomen delendum*).

3. Caucasian bear, *Ursus (Ursus) arctos meridionalis* Middendorff, 1851 (synonyms *caucasicus*, *dinniki*, *smirnovi*, ? *persicus*; the designation *syriacus* was also applied to this form).

Dimensions moderate and small, very variable in size. In general, considerably smaller than Middle Russian bear, *U. a. arctos*. Pelage slightly fluffy. Coloration lighter than that in Middle Russian form (*U. a. arctos*) and varies from straw-colored to light brown, quite monotone—the range of its variation is less than *U. a. arctos*.

"General tone reddish-brown, comparatively light, without admixture of black and brown tones. Light frosting of tips of guard hairs quite weakly expressed, and only on anterior part of body. Underfur, light or light-chestnut. Guard hairs are brownish-reddish, with very short light tips or without them. Limbs and abdomen

same tone as body and not darker than it. Muzzle somewhat lighter than trunk, tips of ears same tone or slightly lighter than trunk. Sometimes, collar occurs, developed slightly more strongly than in *U. a. arctos*, in the sense of covering the neck. Coloration of some individuals entirely monotone. Tail same tone as trunk" (Flerov, 1935). On withers, where hair is greatly elongated, a dark area (spot) is evident, emphasized by somewhat darker color of underfur. Here, thanks to "disarray" of guard hairs, it [underfur] is more easily seen.

Light and dark color types not sharply manifested. Darker animals encountered relatively rarely, and deviations from more broadly distributed, above-described type fall primarily on the side of further lightening.

Greatest length of skull in male is 303–394 mm; condylobasal length, 288–353 mm; length of upper toothrow, 110–133 mm.

Great Caucasus, Trans-Caucasus except in south and southwest and Talysh—on the south including northern Armenia and excluding coastal district of Black Sea northwards to Sukhumi region.

Outside USSR; absent.

The Caucasian form of bear is very unique and of great interest. Various, entirely different, opinions have been expressed about it (Middendorf, 1851; Dinnik, 1914; Satunin, 1915; Smirnov, 1916; Ognev, 1931; Adlerberg, 1935, Flerov, 1935).²⁹ The extreme points of view on one side assume the presence of four forms in the
 432 Caucasus (Smirnov, 1916; Ognev, 1935), and on the other assigns bears of the entire Caucasus to one form; *U. a. syriacus* (Adlerberg, 1935).

While there is comparatively little color variation, the Caucasian bear is distinguished by very great and complex variation in general dimensions and skull; the latter are extraordinarily variable both in size and structural characteristics. In the Caucasus, there is a very large bear, not smaller, or only a little smaller than in the north, having a large, massive skull with sharply developed protuberances, crests—etc. of the same type as in the Middle Russian *U. a. arctos*.

²⁹Except for Pocock's (1932) paper, no original studies deserving of attention are found in foreign literature. Authors commonly agree with the viewpoint of one or another of our investigators, often Adlerberg (1935), probably because it is the simplest.

This is the type "*caucasicus* Sm.". Its similarity to the northern type is so great, that some authors (Dinnik, 1914; Satunin, 1915) accepted the existence in the Caucasus of the nominal (*U. a. arctos*) northern form of bear. Greatest length of skull of male of this type is 348—M 368—394 mm. Some individual skulls are even larger than in the eastern Siberian *U. a. yeniseensis*. Equally with this, in some places in the Caucasus, there is a small animal, having a small skull of the infantile type—with large braincase, weak crests, narrow zygomatic arches, etc. (type "*meridionalis* Midd."), living side by side with them. Between these extreme forms, all transitions occur (in part this is type "*dinniki* Sm."). Such sharp qualitative and quantitative variation gave grounds, with a purely morphological approach, to their understanding of species and race, for the description of various forms of bears in the Caucasus.

In the distribution of these types, there are some geographical regularities. In the Main Caucasus range live bears of all three types. They are found together (attempts to find ecological differences between them were unsuccessful). However, large animals (*caucasicus*) occur more frequently in the middle, and especially in the western, parts of the range. In the Trans-Caucasus, the large form is absent, and bears met with here are of moderate and, mainly, small ("*meridionalis*") types.

Several geographic tendencies in color also exist. In the Main range, together with light, a significant number of relatively dark animals are encountered. In the Trans-Caucasus, such dark animals are few, and light and very light predominate. In addition, there is no sharp geographic localization, and mutual exclusion of different geographic types. This is one race, which is, however, entirely variable, not only in qualitative, but in part in quantitative, features. There are only demonstrated tendencies in geographic displacement of types of variation (see below, description of Syrian bear).

This picture of characters and their distribution in the population directly indicates that the Caucasian bear, *U. a. meridionalis*, itself represents a transitional, apparently, hybrid race from the European-Siberian group of bears (*arctos*), namely *U. a. arctos*, to the Near Eastern group of bears (*syriacus*), namely *U. a. syriacus*. Named thusly, this should, probably, decide the "enigma" of the Caucasian bear.

Clearly unfounded is acceptance of several forms, as was already previously shown. However, so too unfounded is assignment

of all Caucasian bears to *U. a. syriacus*. As this form is not badly known, it is certain that bears of the Great Caucasus as a population have very little in common with it. They differ from it, and from animals of the greater part of the Little Caucasus and Trans-Caucasus (except the south; see below, description of Syrian bear). As for the detail, that in the Trans-Caucasus there occur large numbers of smaller and lighter animals, and few large and dark ones, this is entirely regular. In the Trans-Caucasus, the features of transition to *U. a. syriacus* are more evident, and the genetic induction [sic] of this form is naturally greater than in the Great Caucasus.

The data given about character traits of *U. a. meridionalis* and geographic tendencies of their distribution in the population are useful in understanding its other characteristics and their origin. As it is known, the Caucasus, and particularly the Trans-Caucasus, received its fauna, which is forest-associated to a considerable degree, from the Near East and Asia Minor or from Europe through
 433 Asia Minor. Probably the colonization of the Caucasus by bears also came from the south. Thence, apparently, small, light bear penetrated. This possibility exists at the present time. On the other hand, in the past, even recently (Holocene), large and dark bear also penetrated into the Caucasus from the north.³⁰ This penetration came from the northwest—from the Don to the Kuban’.

The mixing of these two lineages by unlimited hybridization gave the existing variegated morphological and geographical picture of the race. With this viewpoint, the presence of large, dark bears (as well as small), mainly in the Great Caucasus and especially in the west, and the predominance of small, light ones in the Trans-Caucasus is explained. It is noteworthy that in the Caucasus there are bears whose skulls do not differ from *U. a. arctos*. Therefore, *U. a. meridionalis* is a transitional form between the northern—European-Siberian—and the southern—Near Eastern bears. Its “polymorphism” is the result of its hybrid formation. This form occupies a considerable and zoogeographically distinctive territory, well characterized, and therefore deserves to be considered in the nature of an independent subspecies.

³⁰A similar possibility was already assumed by Smirnov (1916). Adlerberg (1935) is completely wrong in his affirmation that “in any case . . . there is no basis for arriving at the conclusion reached by Smirnov, that the bears of the Caucasus speak to the influence on such a fauna of boreal character” (p. 100).

The Caucasian bear is, to a certain extent, analogous to the Eastern-Siberian *U. a. yenseiensis*; however, the whole picture here is apparently more sharply manifested; in particular, amplitude of variation is greater.

Note. Adlerberg (1931) suggested elimination of the name *meridionalis* Middendorf on the basis that Middendorf understood under this name, not only the Caucasian bear, but also bears of Asia Minor and southern Europe, and that the skull of a small form of bear served as type. This author suggested the name *caucasicus* Smirnov, 1916 be employed for the described form. From a nomenclatural viewpoint this argument is entirely unconvincing. Middendorf (1851) gave the characteristics and distribution, in which he first mentioned Caucasus, and the name given by him is formally irreproachable. Adlerberg's mistake was repeated by other authors following him (Bobrinskii, 1944; Novikov, 1956).

Near Eastern bears—group syriacus

4. Syrian bear, *Ursus (Ursus) arctos syriacus* Hemprich et Ehrenberg, 1828 (synonym *lasistanicus*).

Dimensions small—not larger than small individuals of the Caucasian bear (*U. a. meridionalis*); on average, somewhat smaller. Fur short, sparse and coarse. Color very light, predominantly straw-colored, legs not darker than trunk. Hair on withers long, having gray-brown base and short light tips, from which a relatively dark area is formed here. In some individuals, dark stripe extends along spine. Main color types are two: darker, sometimes approaching in color the light form of Caucasian bear (*U. a. meridionalis*). Animals of light type, which are a majority, are significantly lighter. They often have whitish fur, with characteristic development of straw yellow or sometimes even rosy tones (very lightest animals occurring are similar in color to polar bear; Adlerberg, 1935).³¹ Claws brownish-horn with dark tips.

There are no data on craniological characteristics and dimensions. Weight not more than 190 kg (Armenia; Dal', 1954).

Black Sea coast of the Caucasus northward to Abkhaziya (Sukhumi region), southern Trans-Caucasus south of Lake Sevan

³¹"White bears" which sometimes appeared in the arena of the Roman circus were, apparently, such very light animals of this form (Satunin, 1915).

(in particular, Sisiansk, Megrinsk, Kafansk and Goriisk regions of Armenia; Dal', 1954), Karabakhsk range, districts west and south-
 434 west of Sevan (slopes of Mt. Aragats [Ararat]), Talysh and Kopet-Dag.

Outside the USSR—Palestine (exterminated), Syria (partially exterminated), Lebanon, Asia Minor, Iran.

U. a. syriacus is a very poorly studied form overall. This particularly applies to animals living within the borders of the USSR. Direct comparison of materials from there with "typical" *syriacus* has not been done by anyone. At the same time, differences between bears in our above-mentioned regions and the other forms in the Soviet Union are adequately determined. The characters of *U. a. syriacus* from other parts of the range are also poorly known. Bears are extinct in a series of places, are generally rare, and there are few in museums. The main character of the race is, apparently, the very light color and small general dimensions of body and skull.

Animals from the Pri-Caspian province of Iran and Kopet-Dag (and, probably, from southern Trans-Caucasus and Talysh) are affiliated by several authors (Flerov, 1935) to the Caucasian *U. a. meridionalis*. Judging at least by bears from Kopet-Dag (Ognev, 1931; V.G. Heptner), this is incorrect. It is possible, moreover, that animals from northern Iran and Kopet-Dag are not fully "typical" compared to those of southern Iran and Syria. The most recent investigations associate all the bears of Iran to the described form (Misonne, 1960). The limits of distribution of this form in the Trans-Caucasus on the north are not sufficiently clear. Forest districts in the mountains of northern Armenia (north of Lake Sevan) and northwest of there were, apparently, occupied by large Caucasian bears (Dal', 1954). It is also not known how deeply into the Caucasus from the seashore this bear is distributed, and which form inhabits the Trialetsk, Adzharo-Imeretinsk ranges and adjoining places, etc.

5. Tien Shan bear, *U. (Ursus) arctos isabellinus* Horsfield, 1826 (synonyms *leuconyx*, *pamirensis*; the species epithet *pruinus* was applied to bears of this form living among us).

Size is quite small or moderate. Pelage soft, long, shaggy and somewhat sparse. Color very light, varying from light-straw (whitish) to light grayish-brown. Coloration monotone, extremities and tail not darker than trunk; ears very light, whitish, always lighter than general color tone. Developed collar occurs. Claws light.

Two main color types exist, connected by a complete series of transitionals. "Light type: general tone reddish-straw or brownish-white with translucent light sandy-sandy underfur. Muzzle light, straw-whitish, hairs on forehead have dark base. On neck, shoulders, nape, and band along anterior part of spine, the hairs have brown, quite dark, base, but lighter tips than on other parts of body. Ears very light, tone of muzzle lighter than general color tone. Belly darker than upper trunk, hairs here do not have light tips.

Dark type: general tone light, rosy-brown, extraordinarily homogenous with a well manifested light frosting. Muzzle is somewhat more reddish than trunk. Ears very light in color, straw-whitish, lighter than whole body. Belly slightly brown, but becoming darker dorsally as are extremities. Tail same tone as trunk. Underfur quite dark, rosy-brown. Hairs have small light tips (Flerov, 1935).

Accurate data on the dimensions of this form within the boundaries of the USSR are actually absent. An old male from the Chatkal range had a 140-cm body length, height at withers, 90 cm; length of hind foot, 20 cm. Greatest length of its skull, 365 mm; condylobasal length of skull, 320 mm; zygomatic width, 195 mm (Sludskii, 1953). In general, skull length may reach 383.5 mm; condylobasal length—356 mm, zygomatic width—233 mm (Ognev, 1931; one specimen), i.e. as in Middle Russian *U. a. arctos*. In the population, very small individuals are more frequent in the south, analogous to the small form of the Caucasian bear *U. a. meridionalis*, but they are rare to much more rare than in the Caucasus. The type "*U. pamirensis*" is assigned to them. Great-
 435 est length of skull, 279.5 mm; condylobasal length 261.3 mm; zygomatic width, 172 mm (Ognev, 1931).

Mountains of eastern half of Middle Asia—Pamiro-Alai system and Tien Shan eastward to the Ili river.

Outside the USSR—contiguous parts of Pamiro-Alai and Tien Shan in China (limits of distribution eastward not known), western Himalayas from Chitral in west to Nepal in east, Karakorum (?), Waziristan, Afghanistan.

U. a. isabellinus is a well-defined form, close to *U. a. syriacus*. Their characters overlap and the differences of both forms are insufficiently clear. Sometimes they are united as one (Flerov, 1935) which is, apparently, incorrect. Their ranges in western Afghanistan and eastern Iran are separated from one another. In the northeast, *U. a. isabellinus* integrates with the European-Siberian

U. a. arctos. In the Dzhungarsk Alatau lives an intermediate population, and animals with several such characters (light color) are encountered in the southern Altai (Sludskii, 1935). *U. a. isabellinus* is also very clearly distinguished from the Tibetan *U. a. pruinosus* in craniological features, and its placement in this group (in "species" *pruinosus*; Ognev, 1931) is ungrounded. The boundaries of the ranges of these two forms in relation to each other are not known. In Tibet itself lives only *U. a. pruinosus*.

The southern (Kashmir) representatives of the race are, possibly, in general somewhat smaller than the northern (Tien Shan); however, the difference is negligible and the bears of Tien Shan should not be considered a separate form (*leuconyx*) (Pocock, 1932, 1941).

Far Eastern bears—group piscator

6. Kamchatka bear, *Ursus (Ursus) arctos piscator* Pucheran, 1855 (the epithet *beringianus* is often used with reference to this form; see below).

Measurements very large. Pelage long, dense and soft. Color dark, predominantly dark brown; lighter color type rare. Limbs always darker than trunk. Skull very large and massive, with broad forehead region, which is quite steeply elevated above nasal bones. Nasal bone relatively shortened, nasal opening broad; cheek bones very widely disposed. Articular processes very wide; teeth relatively small. Claws dark.

Dark type. General tone of fur saturated, dark brown; in extreme cases blackish-brown with dark violet-bluish tint or even almost coal-black. Admixture of dark chestnut tone on head, in region of shoulder-blades and along back. Extremities dark-brown with dark violet tone.

Light type. General tone of fur brownish-reddish and even golden-yellow, depending upon width of light tips of hairs on occiput, shoulder-blades and back. Sides of the head, withers and limbs dark, cinnamon-brown. On the whole, bears of this type colored quite variably. Lightening of color may be more intensive, and may cover great part of trunk; limbs always dark.

Between both color types, there are all transitional forms. Extreme forms of the light type are encountered in the form of rare

exception, extreme forms of the dark type—much more often.

Maximum body length reaches 240 cm, height at the withers, 135–140 mm, weight 650 kg and perhaps more.

Greatest length of skull of males 326–M 403–436; of females, 325–M 357–397 mm; condylobasal length of skull of males, 348–M 372–386 mm, of females, 303–M 354–370 mm; zygomatic width of
 436 males, 212–M 258–277 mm, of females, 200–M 216–242 mm; length of upper toothrow of males, 133–M 136–145 mm and of females, 119–M 126–133 mm.

Found in Anadyr territory, Kamchatka, Karaginsk islands, Kuril islands, Okhotsk coast southwards to Stanovoi range and Shantar islands inclusive. Extension of range deep into the continent is not known.

Outside the USSR—Saint Lawrence Island and the Bering Sea.

The Kamchatka bear is a well-characterized race, related to a number of the largest forms of the species as a whole. It differs from bears of the group *arctos* very visibly, although as is known, it is linked with *U. a. arctos* through the east Siberian form *U. a. yeniseensis*. The limits of the range of both forms are unclear; in some places, for example in Anadyr territory, both very large typical *U. a. piscator* and also bears of smaller dimensions very similar to *U. a. arctos*, are encountered. The relationship of *U. a. piscator* to the form *U. a. lasiotus*, which systematically is closest to it, is not yet sufficiently clarified. This applies both to characters and also to distribution.

The Kamchatka bear is also very closely related to several bears of Alaska and northwestern America (*gyas-middendorffii* group). It is a single group of closely related races, characterized by very large size (maximum for the species) and the above-mentioned peculiarities of the skull. Relationships of all Pacific Ocean forms among themselves is, apparently, much closer than is now believed. In particular, assertions of differences in measurements (American are larger), are, apparently, exaggerated (see below).

Note. Instead of the name *piscator* Puch., employed for the described form by Ognev (1931), in the last decades several Russian, followed by foreign, authors (Adlerberg, 1935 a; Bobrinskii, 1944; Novikov, 1956; Ellerman and Morrison-Scott, 1951, and several others) began to use the name *beringianus* Midd., 1853. In this case, they refer to the Sibirische Reise of Middendorf, where in the second part of volume II, in figs. 1–6, is illustrated a skull of

"var. *beringiana*". As already noted by Ognev (1931), it originated from Malyi Shantar Island. Ognev suggested considering this specimen as the type of the form, and consequently, the type locality is (some authors refer to B[ol'shoi]) Shantar Island; Ellerman and Morrison-Scott, 1951). Ognev (1931) also showed that Shantar bears belong to the Kamchatka form, and therefore it seemed that denial of the name *beringianus* was not logical.

Authors using the name *beringianus* put out of sight that the description in "Sibiris[c]he Reise is the second description, the first having already been given in 1851 and in it for "var. *beringiana* the following was stated: "distributed in the north, and especially in northwestern America and in the countries of the whole eastern coast of Siberia, including Manchuria and the Japanese Islands". Therefore, Middendorf, under the name var. *beringiana*, envisioned all large bears of the Pacific Ocean districts of both continents. However, it is indisputable that under contemporary nomenclatural rules, the name *beringianus* belongs to one of the forms of northwestern America, apparently, in Alaska (it must, seemingly, replace the name *middendorffii*).

The first name after 1851 may be considered that of Pucheran-*piscator*—in 1855. This name is more suitable because it was given to the population of Kamchatka, where the animals are very typical. The Shantar islands are located on the very edge of the subspecies ranges, and the beginning of the region inhabited by the form *lasiotus*, where a mixture of the two forms are noted.

7. Ussuri bear, *Ursus (Ursus) arctos lasiotus* Gray, 1867 (synonyms *mandchuricus*, *cavifrons*; the species epithet *yessoensis* was applied to some populations of this form).

In all respects similar to the Kamchatka bear, *U. a. piscator*, but distinguished from it by somewhat more elongated skull, less elevated forehead, somewhat longer nasal bones and relatively less widely separated zygomatic arches. Teeth more massive, second upper molar more elongated. Fur color as a whole somewhat darker—light-brown to black.

Greatest length of skull of males, 387–M 423–455 mm; condylobasal length of skull, 360–M 394–418 mm; zygomatic width 236–M 251–277 mm; length of upper toothrow, 137–M 145–151 mm.

437 Found in Ussuri territory, Sakhalin, Pri-Amur, northwards to latitude of Shantar islands and, perhaps to Stanovoi mountain range, and southern Kuril islands.

Outside the USSR—in northeastern China (former Manchuria), Korean Peninsula, and Hokkaido Island.

Attribution of bears of the Mongolian Republic to this form (Ellerman and Morrison-Scott, 1951) is incorrect.

Differentiation of Ussuri bears is not great, but real. Animals may attain, apparently, a somewhat larger size than even Kamchatka [bears].³² The separation of Sakhalin bear as a different form (*Ursus yessoensis*, Ognev, 1931) is, probably, not justified. Range limits, in respect to the Kamchatkan *U. a. piscator* and eastern Siberian *U. a. yeniseensis* are not clear. Apparently, sufficiently wide regions of transition exist in Pri-Amur, and perhaps, in Trans-Baikaliya.

It is sometimes asserted that in Ussuri territory and in Pri-Amur where the above-described form of brown bear is found together with the white-chested (black) bear (*U. thibetanus*), hybrids of these forms occur. This opinion is mistaken, and is based on there being, among Ussuri brown bears, almost pure black individuals (Bromlei, 1956).

Outside the borders of the USSR, in the Old World, except for those enumerated which are within our borders, and *U. a. crowtheri* Schinz, 1844 (see above), there is only one other race—*U. a. pruinosus* Blyth, 1854—of Tibet, western parts of Gansu and Sichuan, Kam, eastern Himalayas, and extreme southern M[ongolian] P[eople's] R[epublic] (?).

Concerning American races of bears, they are discussed above (V.H.).

Biology

Population. Within the boundaries of its contemporary range, populations of brown bears are distributed very unevenly. This depends not only upon the extent of forests in separate parts of the range. The bear is not simply a forest animal but an animal of large forest

³²The largest skull of the described form given by Ognev (1931) is only slightly less than the maximum size of the world record (Alaska, according to Haltenorth and Trense, 1956). If we take into consideration that in our country up to now, "records" are not given any attention, and the hunters, and especially traders, do not generally collect skulls as trophies, it is possible, perhaps, to consider that animals of the described form (and also Kamchatka) attain dimensions of large bears of America).

massifs. Its numbers depend also upon the degree of forest development by humans (disturbance), and also upon differences in food productivity (in general and by season). Of great significance is direct pursuit on the part of humans.

Data on present populations are insufficient, and of an approximate character. Figures on the state of tanning are not indicative of numbers, since brown bears are taken episodically, and their skins often remain with hunters (no fewer than 60%).

In 24 districts in the middle zone of the European part of the RSFSR, the minimal number of bears is about 4,000 (S.G. Priklonskii and V.P. Teplov). The territory investigated covers, in the north, Kirov and Kostromsk—in the south—Lipetsk and Tambovsk, in the West—Smolensk, Bryansk and Kalininsk districts, and in the east—Udmurtiya and Tatarsiya. (The above-mentioned figure is obtained by extrapolation for the whole forested area of these districts from a figure of 2,058 individuals; this latter was obtained by summing data of a series of *leskhoz* [forest cooperatives], with an adjustment of 25–30% for the possibility of duplication of the data of mixed *leskhoz*). Ninety percent of the above-mentioned population applies to the northern zone of this territory. Of these, 54% applies
 438 to northern Kirov district and Udmurtiya, and to eastern Kostromsk district. About 24%—to the Trans-Volgan part of Gor'kovsk, Ivanovsk and Yaroslavsk districts, and to Chuvash and Marii ASSR. The remaining 22% fall within the northwestern part of Smolensk district, Kalininsk district, and Nekouzsk region of Yaroslavsk district.³³ Very cautious extrapolation of typical densities gives 10–12 thousand for the districts of the European north, and for the districts of the northwest, about 6,000 bears. In Estonia, about 180 bears have been counted, and in Byelorussia, about 80 (Serzhanin, 1955). Therefore, the estimated population of brown bears in the European part of the USSR (excluding the Caucasus) hardly exceeds 22–23 thousand.

Population density (per 100 hectares of forest) is a very important item in estimation of the bear's living conditions. In the recent past, the highest density was observed in Kamchatka, in the Kronotsk preserve—9–15 per 10 km². Along a 10-km route in montane, berry-bearing tundra, one may encounter up to 15 bears (Averin, 1948).

³³All these figures are very approximate and give only very general indication of populations and their sizes.

From 1940 to 1948, as a result of direct destruction, the bear population in Kamchatka decreased catastrophically. A considerable density—from 1 to 3 bears per 10 km² (1000 hectares) is characteristic of montane forests of Sikhote-Alin', the Caucasus preserve on the northwestern slopes of the Main Caucasus range (Nasimovich, 1940), the Pritelesk part of Altai preserve (Yurgenson, 1938), and also upland taiga on the right bank of the Yenisei [river] ("Stolby" preserve). High density, with annual fluctuations from 0.4 to 0.9 per 10 km² is characteristic for the Central Forest preserve (southwestern part of Kalininsk district; Yurgenson, 1937).

Moderate densities on the order of 0.25–0.40 are typical for taiga forests on the upper Pechora and Ilych rivers (Teplov, 1960), in the basin of the Konda and Sos'va rivers (data from Kondo-Sos'vinsk preserve), southern Sakhalin (V.O. Shamykin), and for the territory of the Altai preserve as a whole (G.D. Dul'keit). In the European part of RSFSR, the forest along B[ol'shaya] Koksha (upper Volga, Kalininsk district) represent an example of moderate density—0.25 [per 10 km²] (Stroganov, 1934).

In 24 districts of the RSFSR, moderate densities have been determined within a range of 0.03 (Meshchera) to 0.35—for the northeast of the territory. For the northern zone of this territory, a density of 0.20–0.35 is characteristic. For the Prisursk section, the centre of Kirov district, and the southwestern part of the territory (Bryansk district, southwestern part of Kaluga and Tula, and the northwestern part of Orlovsk districts), typical density is on the order of 0.10–0.17; for the central districts of the given territory—0.03–0.08 (S.G. Priklonskii, V.P. Teplov). In Estonia, density reaches 0.15. An example of low density (0.12) might be the forest of the Lapland preserve (O.I. Semenov-Tyan-Shanskii).

In national parks of the USA (Yellowstone, Glacier) a bear population density of 0.28–0.29 is estimated as moderate. In Romania, densities of 0.31 to 1.0 prevail; less than 0.3 is characteristic for 1/3 of the hunting areas. Here there are hunting reservations with a density above 1.1 (Almeshan, 1962).*

Habitat. Brown bear habitat within the boundaries of the USSR is variable. In flatlands, it is, first of all, a forest animal; in the extreme North, a periodic inhabitant of open tundras. In mountains,

*In Lit. Cit., given as 1963—Sci. Ed.



439. Fig. 155. "Bear crack" (Ayu-Ter)—habitat of Tien Shan brown bear, *Ursus arctos isabellinus* Horsf. in the mountains of Tersk Alatau. Tien Shan. Here, there are also Siberian ibex [*Capra sibirica*], gray marmot [*Marmota baibacina*], and snow leopard (ounce) [*Uncia uncia*]. June 1964. Photograph by G.I. Zubanov.

it may be found both in forests, and also in high-montane meadows, as well as among montane tundras. In Kamchatka, Sakhalin and the Primor'e, a considerable quantity of bears restrict themselves to the littoral of the sea coast at particular times of the year.

439 The bear prefers small-leaved coniferous forests. Among conifers, it prefers forests with dark conifers—spruce, fir and nut pine, but does not avoid pine woods and larch stands. This is explained in that even in pinewood regions, dark conifer trees are closely associated with taiga forest glades with numerous tall plants* and also with tall-grass* vegetation along the banks of forest streams and creeks, which serve as the main feeding places of this animal. Owing to historical causes, the bear is linked to broad-leaved forests only in the Caucasus, Primor'e territory and in parts of the Carpathians.

Since activities of bears in their active period occupy an area quite considerable in its extent, it cannot be restricted to any one stand or type of forest, but only to a combination of them. This occurs because each inhabited area must include feeding stands, resting places, and migration routes. There are also winter den sites, usually found outside the borders of the permanently inhabited area.

440 Often, the various sites needed by bears are scattered in separate sections among stable "migratory routes". Thus, in the Pechora taiga, in mossy, dark coniferous forests with berry bushes, traces of bear activity amounted to 26% of occurrences, in pinewoods—23%, in taiga glades with tall vegetation* along the banks of creeks and rivers—28%, in open sphagnum bogs—8%, in birch groves—7%, in grassy fir stands—4%, in unregenerated burns—2%, and in high-montane areas—2% (Teplov, 1960). In the various months, the bear prefers different biotopes: in April–May and in October—mossy, dark coniferous forests and pinewoods, in June–July–August—taiga glades with tall vegetation, then dark coniferous forests and pine groves; and in September, again glades and sphagnum bogs.

Food. Geographic and seasonal variation is well demonstrated in the food of the brown bear.

Spring is the most difficult and severe period occurring for the bear, particularly early, until [growth of] vegetation begins. It is particularly difficult for bears where they emerge from dens when the snow cover is still deep (Kola Peninsula). In this case, the animals in April and May feed mainly on ungulates (elk and

*In the Russian original the words *krupnotrava* and *bol'shetrava* both are used here—what distinction the author wishes to make, if any, is unclear—Sci. Ed.

reindeer), attacking the living [animals] and eating carrion. Ants and their larvae also occur as a permanent element in their food (they excavate exposed ant-hills). In the upper Pechora, in April and May, ants and their larvae comprise their main food (Teplov, 1960; P.B. Yurgenson). Remains of vertebrates and nut pine "nutlets" [seeds] are met with in small quantities in their excrement. In the Denezhkin Kamen region in the Urals, cases were noted of attacks on reindeer and hunting at capercaillie display-places.

In middle Sakhalin in spring, bears feed on the previous year's red billberry, ants, and marine flotsam (pinnipeds, fishes) and at the end of the period—on shoots and rhizomes of tall grasses. On the southern part of the island (V.A. Shamykin), marine flotsam is of greatest significance (fishes, molluscs, holothurians), as well as insects and maple twigs. In the Sikhote-Alin' r[ange] in Primor'e in spring, bears feed on the remains of the harvest of acorns, Manchurian walnuts, and seeds of Korean nut pine (G.F. Bromlei, Yu.A. Salmin and V.D. Shamykin). During famines, they feed on the red billberries of the previous year. In years with poor harvests, besides nuts and red billberry, they also capture insect larvae, wood-boring ants and, later on, roots of *saran* (lily) and the first shoots of graminoid vegetation. In Kamchatka (Averin, 1948), where the spring period in the bear's life lasts from April to about June, at first its food consists of the previous year's litter—especially stems of rough blue-joint reed grass [*Calamagrostis langsдорфи*] and appearing later, new shoots of willow, *Silau*s, meadowsweed [*Spirea*] (*shelomainika*)* and large umbelliferous plants. The widely distributed reed-grass continues to be particularly significant, and, among berries, the previous year's cones and overwintering "nutlets" [seeds] of prostrate nut-pine. As in Primor'e and Sakhalin, marine flotsam, particularly the dead young ringed seals [*Phoca hispida*], are of great importance in this period.

In the northeastern Altai, in April–May, the bears in forest glades of sun-warmed slopes feed on roots of dog-tooth violet [*Erythronium*], young shoots of *puchok* (cow parsnip) [*Heracleum*], angelica, cotton-thistle [*Onopородон*], and lungwort [*Pulmonaria*] as well as horsetail and reed-grass (Yurgenson, 1938). In forests of the middle zone, in April–May, serving as bear foods are the previous year's whortleberries (in mossy bogs), green shoots of young aspen and

*Local word?



441 Fig. 156. Nut pines at the upper limit of the forest and tall-grass montane
meadows in mountains by Teletsk Lake—a feeding place for bears. Altai
preserve. Photograph by G.D. Dul'keit.

mountain ash, young sprouts of lungwort, and lichens from willow bushes in mossy bogs of stunted trees—*omshara** (Yurgenson, 1937).

In the northwestern Caucasus the main spring foods consist of beech and oak mast (rarely chestnut and filbert), stems and leaves of grasses, cow parsnip and coltsfoot, ants, beetles and their larvae (Nasimovich, 1940). In some places, attacks on chamois occur.

A break in food comes on in May, when bear pastures appear. The first period of summer, before the mass ripening of various berries, is characterized by uniform feeding, in which stems and
442 leaves of tall forest vegetation are utilized—first of all umbellifers: cow parsnip, garden angelica, wild angelica, and others. In the Far East and Caucasus, coltsfoot [*Pedasites*] or bear burdock [*Arctium*, *Lappa*] is eaten in great quantities, as is sow thistle [*Sonchus*] or cotton-thistle, ramson [*Allium ursinum*]; and more rarely fireweed [*Epilobium*], horse sorrel [*Rumex confertus*] (Pechora), cottongrass

*Local word—Sci. Ed.

[*Eriophorum*], marsh hawksbeard [*Crepis paludosa*], Sakhalin calla, aspen leaves, and sprouts of huckleberry are widely utilized and in great quantities. In the mountains of Sikhote-Alin' bears strip off the bark of the white-barked fir and feed on its cambium and sap. As in spring, bears continue to breakup rotten stumps and logs and eat wood-boring ants and their larvae as well as the larvae of long-horned beetles, wood-boring beetles, and weevils. Geographical differences in feeding in this period are not great.

In the second half of summer, the essential role in the forest of tall vegetation is retained, but fruit shrubs and bushes acquire great importance. All over the whole taiga zone, and in forests of the middle zone, huckleberry occupies chief place in bear's food, and in second place, raspberry, but the period during which it is eaten is not prolonged. Among other berries, bears often eat blueberry, rarely cloudberry (Pechora) and crowberry (Kola Peninsula, Kamchatka), and along Sikhote-Alin'—berries of honeysuckle, yew, *Actinidia*, Amur grapevine, and buckthorn; on southern Sakhalin—current [*Ribes procumbens*] and chokecherry. On middle Sakhalin, salmonid fishes comprise up to 28% of the bear's food in August.

In Kamchatka, from the beginning of July, among berries they eat blueberry and crowberry (*shiksha*). Already beginning in July, humpbacked salmon, salmon trout and other salmonid fishes ready for spawning in the rivers by degrees acquire great significance. Feeding on graminoid vegetation continues; some bears do not go down to rivers at all and do not eat fish (Averin, 1958).

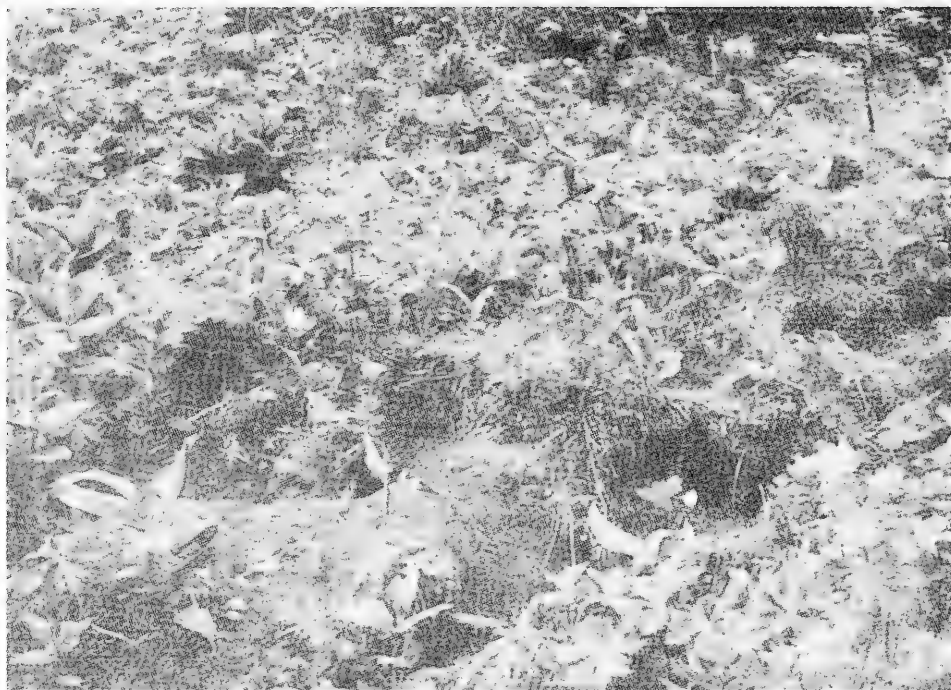
In the northwestern Caucasus, from the middle of July, raspberry appears in the food of the bear, followed closely by blackberry and current (Nasimovich, 1940). Later—green apples, cherry plum, 443 pear and sweetcherry. In rare cases, attacks on chamois were observed. Significantly more frequently it feeds on carrion. In the course of the summer, bears continue to feed on tall vegetation, and eat beetles, and ants and their larvae.

Autumn is the most important period in the nutrition of brown bear since, particularly at this time, fat accumulation takes place which is necessary for successful hibernation. In the majority of taiga regions, it is secured by feeding on berries—whortleberry, red billberry, cranberry, crowberry and others. In years of poor [berry] crops in the Pechora taiga, late retreat into the den has been observed (Teplov, 1953), wanderers are encountered and cases of cattle attack become more frequent (60% of all cases).



441 Fig. 157. Sparse montane forest of nut-pines in Altai preserve. Pasturing place of brown bears; in center of figure, under a nut pine, a bear is grazing. Photograph by G.D. Dul'keit.

Typically, there is a transition from whortleberry and blueberry to red billberry, cranberry and mountain ash in late autumn (from October). The predominance of one species above the others is determined by local conditions. Oats are also a typical early autumn food. Its intensive utilization by bears in Kalinin district lasts for a short time—15–20 days, from the first days of August when the oats are still not fully ripe (Yurgenson, 1937); only rarely are bears in the middle zone not attracted by oat. On the Pechora [river], however, utilization of oats was not observed (Teplov, 1960). For fat accumulation, the period of feeding on oat has, in some places, substantial significance. In the middle zone, a lesser role is played in autumn nutrition by acorns, hazel-nut, ants and graminoid vegetation. In the Urals and in the Pechora basin, in productive years, nut-pine “nut-lets” [seeds] gain importance. The same is found locally both in the



442 Fig. 158. Runways of water voles [*Arvicola terrestris*] uncovered by bear in subalpine meadow. Tele massif, Altai preserve. Photograph by G.D. Dul'keit.

flatlands and in the montane dark coniferous taiga of Siberia. With insufficient food in late autumn, bears in the middle zone feed on plant litter—aspens leaves, dry stems of reed-grass (Yuryenson, 1937). In the oak-groves on the right bank of the Volga, acorns are of great importance (V.A. Popov). In the alpine zone of the east[ern] Altai, bears in autumn energetically dig out the long massive roots of sweet vetch [*Hedysarum*].

Autumn foods of bears in the Far East have their own peculiarities. In Kamchatka, in October–November, they eat “nutlets” of prostrate nut-pine and mountain ash, and salmonid fishes—East Siberian char and silver salmon. In years of famine, marine flotsam gains particular importance, but berries and graminoid vegetation remains of secondary importance (Averin, 1948). On middle Sakhalin, bears in autumn feed on red billberry, “nutlets” of prostrate nut-pine and migrating fish. On the southern part of the island

(V.D. Shamykin)—oats, migrating fish, marine flotsam, *Actinidia* berries, large-fruited sweetbrier, elder-leaved raspberry, shrub mountain ash, rhizomes of coltsfoot and Urukundo maple shoots. In the mountains of Sikhote-Alin' (G.F. Bromlei, Yu.A. Salmin and V.D. Shamykin), from the middle of August, bears *en masse* eat various berries, fruits of Maak's bird cherry, *Actinidia*, Amur grapevine, cork tree, buckthorn, yew, and "nutlets" of nut-pine. They eat great amounts of spawning *sima* salmon [*O. masu*], humpback salmon and chum salmon. In late autumn, the main foods for sustaining fat accumulation becomes nutlets of Korean nut-pine, acorns, red billberry, in part blueberry from bogs and, of salmon—chum. Here, October is the most favorable month for nutrition of the brown bear. In years with deficiency of food, bears more often attack wild boar and roe deer.

On the whole, during the active season of feeding in upper Pechora brown bears, no less than 39 components of plant and animal origin were revealed (P.B. Yurgenson). Of these, according to frequency of occurrence (but not by volume), ants were in first place—32.7%. Then followed fruits—21.3%, of which huckleberry—12.7% and red billberry—5.9%. Vegetative parts of large-stemmed plants constituted 34%, including umbellifers—10.4% (their rhizomes only 3.6%). All mammals constituted only 9%, of which remains of wild reindeers—2.7%; birds—2.7%, including capercaillie—1.3%. Of other food, nut-pine "nutlets" constituted 5.9% of occurrences, wasps—4.4%. Of the individual species of plants with edible green parts; only one large hawkbeard [*Crepis*] (2.6%) and horse sorrel [444 *Rumex*] (3.2%) gave occurrences of more than 2%.

For this period in the feeding of the Middle Russian brown bear (Yurgenson, 1937), animal food constituted 65.4% of occurrences, but according to volume only 38.4%. Invertebrates in this way gave 52.2% of occurrences, and vertebrates—only about 13.6%. Among them, the most frequently occurring were ants—30.7% (by volume only 9.1%). Among plant foods, raspberry occupied the first place in occurrence—44%; then umbelliferous plants—27.7% (by volume—52%). A little lower was the occurrence of oats—23% (by volume, about 50%). Grasses gave 23% of occurrences, and aspen leaves and shoots—9%. This is only a very approximate presentation of the significance of individual food components. In Ussuri territory (G.F. Bromlei), plant food comprised 68.9% of occurrences and animal—31.1%. Among the former, berries comprised 33.9%,

graminoid plants—13.3%, nuts—10.1%; among animal food, insects—16.8%, fish—10.1% and mammals—4% of occurrences.

In Romania, 28 species of plant food and 7 species of animal food were shown for the brown bear (Almeshan, 1962).

Home range. Adherence to a defined home range is characteristic of the majority of brown bears. Such ranges exist even in those cases when bears continuously move widely from one place to another in search of various seasonal foods during the course of the whole period of activity. These movements are not disorderly and are repeated by each animal from year to year in given areas. These quite extensive vast and not strictly limited ranges are particularly typical for bears of mountainous regions—Caucasus, Altai, Sayan, Sikhote-Alin' (Yurgenson, 1938; Nasimovich, 1940; Yu.A. Salmin and V.D. Shamykin).

Bear often stays in a den, outside its permanent home range, since suitable places are not available everywhere. In winter, in sections where there are many places for dens, the concentration of bears may be very great.

Home ranges are well marked, where all conditions necessary for the existence of bear in the forests are concentrated within a limited area—300–800 hectares (Flerov, 1929; Yurgenson, 1931). Dimensions of the range depend not so much on its abundance of seasonal food, but more upon the area of “migratory stations” included within its limits.

Burrows and shelters. During the active period, the brown bear behaves as a typical denning animal. In the northern Urals and Pri-Pechora taiga, its lairs are often found in montane forest meadows and in river floodplains. They are distributed both in open places among tall grass stands, and in the shade of lone standing tree. Lairs also occur along the steep banks of taiga creeks—on the slopes of low, wooded ridges,* among young pines and birches in old burns, and by pine stumps in dry pinewoods. Sometimes, the bear lies up in an ant-hill which it has dug up, and when aggravated by blood-sucking insects, excavates a small hollow in moist ground within a dense riparian thicket of wheat-grass [*Agropyron*] (P.B. Yurgenson).

In the forests of the middle zone, preferred places for lairs are dry elevated zone of “shore ramparts” almost on the very brink of

**Parma*, local word in Urals—Sci. Ed.

the water along remote forest streams, the borders of tall-grass openings, the edges of small forest bogs—mossy bogs and also widely spaced trees and glades with grassy openings, dense thickets of raspberry, young spruce and birch, usually with rotten logs (Yurgenson, 1936, 1937). Bear dens are often restricted to areas of tall grasses and their borders in the mountains of the northeastern Altai (Yurgenson, 1938). In the mountains of the northwestern Caucasus, dens often occur either under overhanging rocks, or on snow fields, and rarely in open alpine meadows (Nasimovich, 1940).

445 Winter hibernacula in forests of the middle zone often occur scattered along the edges of mossy bogs, especially on islands among them, along the shores of forest lake and rivers, with dense growth of mixed forests, among windfalls and near logged areas (Mel'nitskii, 1915). At the same time, the bear does not avoid the vicinity of traveled roads and settlements.

In the upper Pechora (Teplov, 1960), bears prefer to den in pinewoods of the Pri-Pechora lowlands, where snow remains for a less extended time than in the dark coniferous taiga of the foothills and mountains. Of 16 hibernacula, 8 were constructed under overhanging slopes and logs, 6—under the roots of large nut-pines and spruces, and 2—under the roots of young firs and pines.

In the mountains of the northeastern Altai and Sayan (Solov'ev, 1921; Yurgenson, 1936, 1938) hibernacula are predominantly "on the ground", or located in natural caves, rock clefts, and in depressions beneath rocks. Places suitable for this purpose occur rarely, and therefore, groups of dens are frequently occupied by bears for many years in a row. Thus, at Teletsk Lake (Azhi range), within 10 km, 26 dens were found. The majority of dens were restricted to the crests of ranges, the upper parts of slopes, and inaccessible ravines of montane creeks.

In Sikhote-Alin', a better place for a hibernaculum is within the high-montane fir-forest on the northern slopes of hills and on the summits of ranges (Yu.A. Salmin and V.D. Shamykin). In Kamchatka, dens occur in very different places—among large rock fields, under roots and overhanging birch, and in caves (Averin, 1948). Early retiring animals and females build dens more carefully, with a special nest. In Siberia, dens are constructed in montane ravines, in thickets in stands of nut-pines, in coastal precipices, and in the roots of trees. The "bed" is made from the twigs of coniferous trees, leaves, grass, reeds and moss (Middendorf, 1851).

In the northerneastern Caucasus, the great preponderance of bears den deep in the mountains in the dark coniferous forest zone (Nasimovich, 1940). Here, dens most frequently occur distributed along steep rocky slopes—in caves and rock clefts, rarely in holes of large trees, and logs within rhododendron thickets. In the alpine zone (rarely)—in deep caves among limestone rocks. As in the Altai, in this region aggregations of hibernacula may be found—“bear cities” “Above-ground” dens are constructed with one exit in sandy ground, in rotten stumps, near dry stumps, pockets surrounded by small trees, in wind-drifted deposits, under overhanging rocks and in clefts in rocks. In making open dens, bears often excavate tub-like pits with sheer walls which are covered by branches with the tips pointing upwards; in this way, the height of the den can attain 2 meters. Females with *lonchak* [yearlings] (young born in the preceding year) prefer to den in large piles which form an arch, while the pregnant female prefers dense, impassible brushy thickets (Mel’nitskii, 1915).

Nearly every bear lines the hibernaculum with moss, coniferous branches, dry grass, or hay—any material at hand. The quantity of the bedding occurring is sometimes very great. The “brow” of the den does not always face to the south or southwest, as is sometimes supposed. Sometimes, the den opening is plugged with branches, especially in the “above ground” dens having *lonchak*. “*Kurzhak*”—hoar frost above the hibernaculum resulting from the respiration of the animal—is not always observed. The vicinity of the hibernaculum is for the most part “cleared”*; the bear breaks off tree branches which are used for lining the den.

Daily activity and behavior. Most often, in taiga forests and forests of the middle zone, brown bears are active at twilight and night, but on rainy days they usually roam the whole day (Yurgenson, 1937). In the alpine zone of northeastern Altai (Yurgenson, 1938), and in montane tundra on Kamchatka (Averin, 1948), bears are often observed even in the daylight hours, but mainly morning and evening. In the unforested mountains of the northwestern Caucasus in summer, 0.22 bears per hour were observed from 8 a.m. to 10 a.m., from 10 a.m. to 2 p.m.—0.14, and from 2 p.m. to 6 p.m.—0.20 bears; only 0.11 adult bears were observed in the morning hours; during the day 0.04, and in the afternoon—0.20 respectively

*Literally, “broken”—Sci. Ed.

(Nasimovich, 1940). Females with young come out earlier in the hours after midday. On cloudy, rainy days females often graze the whole day. With the passing of autumn in the broad-leaved forest zone, nearer populated points bears become nocturnal animals, hiding during the day in thickets of azalea, rhododendron, laurelcherry [*Laurocerasus*] and ferns or even retreat to day-beds 6–8 km higher in the mountains. In the northeastern Altai (Altaisk preserve) in summer time, bears to a great extent feed in alpine meadows most often during the day. However, during periods of prolonged, extended rain, which are common in these mountains, they do not enter the highlands for many days, keeping themselves lower—in the nut-pines. With the arrival of clear, warm weather, they at once move in significant numbers to the meadows, where they feed for the entire day as if compensating for the omission (V.G. Heptner).

Thus, the brown bear lacks a strict rhythm of daily activity.

Despite its seeming clumsiness, the bear is silent, light and quick in its movement. Seriously frightened, for instance after an unsuccessful shot, it rushes at great speed with huge leaps, extending the hind limbs far forward, and very quickly turning to escape (V.G. Heptner). In walking, its tracks are in a straight line, circling only when fattening, and on approaching the hibernaculum prior to entering into hibernation, but the animal always avoids obstructions and cluttered places. Young bears willingly climb trees—in Primor'e only until they are 1.5 years old (Bromlei, 1956). But where there are many acorns, walnuts or wild bees, the bear does not lose the ability to climb its whole life. In the northeastern Altai, bears obtaining cones with nut-pine "nutlets" often climb to the tops of nut-pines and break off their branches (Yurgenson, 1938). Such damages have been noticed in other regions of Siberia. In Poland, earlier, bears were even caught by snares set in trees; with the decline of wild-bee keeping, bears ceased climbing (Middendorf, 1851).

Bear digs well—in autumn, in digging out holes and the underground storerooms of chipmunks [*Tamias sibiricus*], it excavates deep holes, often in rocky ground. In alpine meadows of the northeastern Altai, it digs up long, thick roots of sweet vetch [*Hedysarum*]. In the middle [forest] zone, in obtaining food, it sometimes lifts up the turf and rolls it into a tube in forest meadows. In the high-montane meadows of the Altai (Altaisk preserve), bears in this way eat subterranean parts of plants and catch voles, "rolling up"

entire large "carpets" (V.G. Heptner). Bears swim well, overcoming distances of up to 6 km and they eagerly bath in hot periods, especially cubs (Yurgenson, 1936, 1937, 1938; Nasimovich, 1940). In order to get rid of blood-sucking insects, they make mud-baths. During periods of drought, they excavate deep holes in mossy bogs in search of water.

As in adult bears, so also cubs rub against tree trunks, leaving their fur as well as claw marks. As early as 1874, the suggestion was put forward that the bear marks its home range by its claws, giving notice to other bears that they were approaching it (Egorov, 1874); quite a bit later, this was also stated by E.T. Seton-Thompson (1911). Even later, the suggestion was advanced that these marks are connected with the breeding period, but this is contradicted—fresh marks are found at various times; and females also make them.

Usually, the bear attacks humans only when it is injured, guarding a fresh kill or when extremely emaciated and hungry [a condition called] *shatun* (in winter). A female, surprised with its cubs by a man, most frequently tries to frighten him by rearing up [on hind
447 legs]. Sometimes, she jumps directly at the person. As a rule, the bear, upon sees a human, flees. Exceptions exist in some districts where they are not pursued by hunters.

Hibernation and winter sleep. A characteristic feature of the biology of bear is winter sleep in a hibernaculum. This is not hibernation as in marmots and similar species, but is a particular sort of shallow winter torpor. In this period, the development of embryos, birth and lactation proceeds in the female. The intensiveness of winter torpor develops gradually, and in the second half of winter, bears are "fast asleep". A necessary precondition for entry into sleep is accumulation of fat deposits in a quantity sufficient for maintaining life in the inactive period, and also in the period of time after emergence from the den early in the spring. In the hibernating bear, the rate of breathing and heartbeat decreases somewhat, and its temperature falls to 29–37°C. Oxygen demand and carbon dioxide output are sharply decreased. The intervals between inhalations become more prolonged and less regular. After 5–10 inhalations and exhalations, a pause of 2 to 4 minutes sets in (Lobachev, 1951).

Bears accumulating fat in timely fashion hibernate earlier. Animals that do not have sufficient amount of fat do not hibernate



Fig. 159. First snow in Altai preserve on balds in Chul'cha basin. Place traversed by bears while going to hibernation places. In foreground, track of animal which has just passed. Photograph by G.D. Dul'keit.

at all (*shatun*) [see prev. pg.] grow extraordinarily thin, attempt to attack animals and sometimes humans, and often die from hunger and freezing.

A necessary act before entering into the hibernaculum consists of complete elimination from the alimentary tract of food remains. In winter, in the rectum, a tight "plug" of wool, dry grasses and other undigested food remains.

Entry into hibernation is preceded by selection and preparation of the hibernaculum. Just before entry into it, the animal obliterates its tracks, and often hibernates before deposition of snow, or at the time of snowfall, which assists in hiding its tracks.

Hibernation does not take place simultaneously even in a single region. Besides degree of nutrition, timing of hibernation is influenced by the yield of principal foods and the particular weather in that year. Entry into the hibernaculum proceeds from the end of

September (vicinity of Krasnoyarsk) to the first days of January (Caucasus; Nasimovich, 1940). Timing of hibernation is obviously influenced by geographic position. Thus, in Kamchatka, the preponderance of bears hibernate at the end of October—females with young, earlier (Averin, 1948). In middle Sakhalin, bears hibernate in the middle of November before heavy snowfalls, in southern Sakhalin (V.D. Shamykin)—at the end of November—beginning of December, in Sikhote-Alin' (Yu.A. Salmin and V.D. Shamykin, G.F. 448 Bromlei)—from the first half of November to the second third of December. In the upper Pechora (Teplov, 1960), based on many years of data, timing of entry into the hibernaculum ranged from 3 October to 3 December—on average about 30th October (Middendorf, 1851).

In the Trans-Caucasus some bears, especially in years with an abundant yield of nuts, do not hibernate on the southern slopes. Mass hibernation here takes place in the middle of December. In the northeastern Altai (G.D. Dul'keit), the period of entry extends from the end of November to the beginning of December (400–1000 *m.n.u.m.*)* and in the years with little food—from 9–10 to 20 December.

The duration of stay of the brown bear in the hibernaculum ranges from 75 to 195 days per year; in the Caucasus—75–120, in southern Sakhalin—135–145, in the eastern Sayan—145–165, in the Kola peninsula and in Kondo-Sos'vinsk preserve—180–195 days. In individual years, it fluctuates significantly. Thus, in the upper Pechora (Teplov, 1960) it equals on average 165 days, with a range from 138 to 190. Therefore, geographic variation in duration of the hibernation period differs somewhat from the multi-year average for a single region.

Timing of emergence from the hibernaculum is determined by various factors: well-nourished animals emerge later than emaciated ones. Early emergence is also associated with an unsuitable choice of location for the den (premature thawing), or disturbance caused to the animal by hunters or tigers (Sikhote-Alin'). In the Caucasus, on the southern slopes of the Main range, the bears are aroused earlier than on the north; in Kamchatka in the interior of the peninsula, later than near the seashore. Females with cubs are the latest to emerge.

**metr nad urovenem morya*; meters above sea level—Sci. Ed.



Plate 4. Middle Russian brown bear, *Ursus (Ursus) arctos arctos* L. Painting by A.N. Komarov.

Bears in the Caucasus are the earliest to arouse, where the earliest date recorded was 5 March, and the average date—14–25 March. The period of concurrent emergence occurs within 10–12 days, and females with cubs leave 9–10 days later (Nasimovich, 1940). Bears on the Kola peninsula are latest of all to leave—about 1 May (O.I. Semenov-Tyan-Shanskii). In Anadyr territory, bears leave at the end of April (Sokol'nikov, 1927), on the Kolyma (Buturlin, 1913) and in Kamchatka (Averin, 1948) where the earliest time was recorded on the 4 April and the latest date—the middle of May (lactating females).

In different regions, there exist significant fluctuations of timing (Table 46). Thus, in the Caucasus preserve, the earliest date observed over 10 years ranged from 5 to 27 March (Nasimovich, 1940) and, in one year (1950), the dates stretched out from 14 March to 18 April (S.I. Chernyavskaya). In Pechora-Ilychsk preserve during 13 years (Teplov, 1960), date of first emergence ranged from 27 March to 25 April (on average about 16 April). In the upper Pechora (P.B. Yurgenson), emergence from the hibernaculum is connected with establishment of favorable daily air temperature and the formation of openings in the ice [of the river]; (with it occurs the arrival of white wagtail and emergence of chipmunk). In this period, thick snow cover also lies over the Kola peninsula. The latest date (for well-nourished animals and lactating females) coincides with the beginning of vegetation growth (first arrival of cuckoos manifests itself as one of the indicators).

Therefore, the boundaries of the USSR, dates of emergence from the hibernaculum range between 5 March and the middle of May, falling primarily in April. The duration of the mass emergence ranges from 6 to 15 days.

Seasonal migrations and transgressions. As a rule, brown bears are sedentary animals, keeping quite strictly to the limits of their home ranges. However, various types of shifts are characteristic for them. Thus, brief local concentration of animals in places of seasonal abundance of one or other food has been observed. In spring and late autumn, middle Russian bears are observed in moss bogs where they are attracted to huckleberries in years of heavy yield. In summer, they are concentrated in hazel thickets, especially in cut-over areas. Early in autumn, a significant concentration, including the majority of individuals, is observed near the oat fields adjoining the borders of forests; they are also noted in oak stands

in connection with the acorn crop (Gor'kovsk district, A.N. Formozov).

More or less regular seasonal migrations are typical for montane regions. Thus, in the northeastern Altai (Yurgenson, 1938) in the active season, bears ascend from the montane valleys to the slopes three times and then descend again, in connection with various dates of ripening of berries and nut-pine "nutlets". In the northeastern Caucasus autumnal migrations are observed from interior montane regions to the borders of the belt of broad-leaved forests and their "fruiteries" (Nasimovich, 1940). These migrations are characterized by great regularity and are associated with the fruiting of oak, beech and other "mast trees", and also fruits growing wild in Circassian gardens. To hibernate, bears again move away deep into the mountains. The distance of such migrations has been determined as tens of kilometers. In the past, bears moved about 120–150 km (Dinnik, 1914).

Such wanderings appear in autumn in Sikhote-Alin' (Yu.A. Salmin and V.D. Shamykin; G.F. Bromlei) and depend upon the yield of acorn, "nutlets" of Korean nut-pine and the distribution of yield

Table 46. Dates of emergence of bears from hibernacula

Region of observation	Date
Lapland preserve	About 1 May
Kolyma territory	End of April
Anadyr territory	Middle of April
Kamchatka	10 April–middle of May
Middle Sakhalin	End of April
Pechora-Ilychsk preserve	27 March–25 April
Denezhkin Kamen	Middle of April
(Middle Ural) preserve	
Ural	Second half of April
Kondo-Sos'vinsk preserve	Beginning of April
"Stolby" preserve	8–28 April
(Krasnoyarsk territory)	
Northeastern Altai	Beginning of April–
(Teletsk Lake)	beginning of May
Southern Sakhalin	Middle of April
Aksu-Dzhabaglinsk preserve	Middle of April
Sikhote-Alin' preserve	End of March–Middle of April
Leningrad and Novgorod districts	20 March–15 April
Central Forest preserve	22 April–2 May
Bashkir preserve	3–11 April

in the area. With a failure of this main, but unreliable food supply, bears here undertake significant migrations of up to 200–350 km.

In the upper Pechora and in the Urals (Sabaneev, 1878; Teplov, 1960) the movements of bears are associated locally with the low yield of berries, and also, on the western to the eastern slopes of the Ural range, is connected with later formation of snow cover there. In Semigrad'a (Kaspaty; Yurgenson, 1936), massive regular migrations from montane forests, repeated every 5 years, are provoked by a heavy acorn crop in the oak forests of the plains. Animals are drawn from the montane forests from a radius of 50–100 km. Coincidence of abundant oak and beech mast crops makes the migrations less intensive, but these are very rare. Bears do not leave regions where the yield of beech mast and blackberry or red bilberry is fruitful (Yurgenson, 1936).

Besides this type of migration, other migrations have been observed which are caused by obligatory situations—major forest fires and summer drought, causing the usual water sources to dry up. Such cases were observed in the middle [forest] zone (Yurgenson, 1937) and in southern Sakhalin (V.D. Shamykin).

Reproduction. According to data of the Moscow zoo (Gulyaev, 1934), rut in the brown bears lasts about 1 month, beginning on 10 May. Individual cases of mating were observed in July. Copulation lasts from 30–40 min. to 1 h. In case of absence of fertilization, estrus is repeated after a fairly long period. Under natural conditions, rut lasts from 10–20 May to the middle of July. In Chita district (Pavlov, 1948), rut in bears coincides with flowering of the coral lily (*Lilium tenuifolium*). The peak of rut at different geographic points takes place at various times within the mentioned time limits but without the clear regularity which has sometimes been mentioned (Middendorf, 1851). Among the signs of rut are shown to be bellowing, fresh conflict, and bite marks on trees, fighting (sometimes ending fatally for one of combatants), pursuit of the female by several males, etc. In the upper Pechora (Teplov, 1960), these signs were not observed at all in June to July, but on the contrary, occurred in the middle of September according to the word of hunters. This coincides with data (Middendorf, 1851) according to which rut extends for several weeks in July–August, but also occurs in May and September. Duration of pregnancy is, therefore, 6 months. According to data of the Moscow Zoo (Gulyaev, 1934), it lasts from 185 to 251 days (8 cases); i.e. 6–8 months, 227 days on average (7.5 months).

Birth most often takes place in the first half of January (Gulyaev, 1934). Individual cases were observed in December, in the second half of January, in February, March and even in April (Middendorf, 1851; Nasimovich, 1940; Stroganov, 1952). In the litter occur 1 to 5 cubs; more often—2, rarely 3; 4 to 5 cubs occur extremely rarely. Young and old females often give birth to one cub (Middendorf, 1851; Gulyaev, 1934; Kuklin, 1937; Nasimovich, 1940 and others). In 1958, in the Kirensk region of Irkutsk district, 5 cubs were found in a den (Stroganov, 1962); in Valdai, 6 embryos were found in a female (Shirinskii-Shikhmatov, 1900).

The sexually mature female bears a litter every other year, since having juvenile cubs, they do not participate in rut. In Caucasus preserve, about 35% of the females have offspring annually (Nasimovich, 1940).

Growth, development and molt. The newborn cub weighs 501–510 g (Gulyaev, 1934), with a body length of 23–23.5 cm. At the age of 14 days, weight has grown to 538–552 g, and body length, 26–28 cm. Newborn cubs are sparsely covered with fur 2 to 3 mm in length, and their eyes are closed. The external auditory meatus is covered by skin. The ear opening becomes defined on the 14th day. Eyes open on the 30th–32nd day. By the third month, it has a full set of milk teeth; by the fifth month the first molar erupts, and in the sixth month, replacement of the milk teeth begins. The last molar erupts at 10–12 months (Adol'f, 1949).

Lactation period lasts about 0.5 year. The cubs separate from the female in their third year of life, having spent the first two winters together with the female in a single den.

Bears grow slowly and full development and growth is not attained earlier than 10 years, and according to some data, 20. A series of changes in skull structure take place until very old age (Zhitkov, 1922). Maximum age of bears in captivity is 47 years. In Bern, a female gave birth to young in her 31st year of life.

Spring molt in the brown bear takes place slowly and is prolonged (Kuznetsov, 1941). In the northeastern Altai, at the end of April–beginning of May, bears are still found in winter fur. In June, in the time of the breeding period, rapid molt takes place. However, autumn molt proceeds slowly and unnoticeably.

Enemies, diseases, parasites, mortality and competitors. Except for hunters, bears have almost no enemies. Primor'e territory constitutes an exception, where the Ussuri tiger may be an

451 enemy, most often attacking bears in winter, in the hibernaculum. Since tigers are almost extinct, such cases are rare and do not have any actual significance. In Caucasus preserve, in June 1931, it was recorded that a leopard killed two small bears. However, this animal is also extremely rare here.

In Primor'e territory (G.F. Bromlei), lynx and wolf may be considered enemies of cubs. There is information on attack by wolves on bears in Kamchatka, but it is not reliable (Averin, 1948).

Competitors of bears are animals that are chiefly herbivorous. Among them are included all consumers of forest berries and nuts, ungulates grazing in forest openings with tall grasses, etc. However, it is doubtful that the activity of these competitors might have vital negative significance for bears.

Concerning the diseases of bears, there is no information. Significant infection with endoparasites has not been recorded.

In an analysis of age composition of 58 bears killed in winter in hibernacula on the upper Pechora (Teplov, 1960), newborn cubs constituted 31% of the whole population, *lonchak* [yearling] (born in preceding year)—12%, and "*pestun*" (to 3 years)—5%. These figures reflect, to some degree, the dynamics of bear mortality at early ages. In the first year of life, it is equal to 61.2%, and in the second—57.2%. On the whole, for the first years it is 85%. These data cannot be presumed to be accurate, but they show that mortality among cubs is very significant and explain the slow rate of growth of the population. If, for the Pechora taiga, juvenile bears were 31%, then in the Central Forest preserve (P.B. Yurgenson), it was in different years from 17.3 to 33.3%, averaging 26.6%, and in the northwestern Caucasus (Nasimovich, 1940), it corresponded to 13.0–31.0%, 23.0% on average.

At an older age, mortality among bears, where they are not hunted by man, is very small, and as a consequence, may attain very advanced age and very large size. In Kamchatka where, in the past, the largest bears weighed up to 640 kg (Averin, 1948), at the present time, animals heavier than 300 kg are not found because of intensive hunting of them.

452 In the Central Forest preserve region, about 11% of the total population are shot by hunters annually (P.B. Yurgenson).

Accidents are another cause of death among adult bears. Cases are known when bears, falling into an opening in the ice, drown or disappear under the ice of rivers and lakes. A series of cases are



451 Fig. 160. Tracks of northern brown bear, *Ursus arctos arctos* L., while walking slowly. Tracks of hind feet do not conceal imprints of fore-feet. Ponazyrevo, Kostromsk district. 5 November 1952. Sketch by A.N. Formozov.

also known when male bears die during fights between one another, and a case of the death of a bear during an attack on an adult elk.

Population dynamics. Changes in number are characteristic for brown bears, but they are poorly known. In the upper Pechora (Teplov, 1960), the number of bears for 9 years fluctuated in a relative index of 1 to 4; with 2–3 short fluctuations between consecutive years. These changes are explained by migrations in years of berry failure. This reason, as well as forest fires and summer drought, cause bears to wander, emigrating and changing numbers in the forests of the southwestern part of Kalinin district (Yurgenson, 1937). Change in numbers is also caused by fluctuations in annual population increase, together with changes in the quantity hunted (including harvest). Thus, in the Central Forest preserve (Kalinin district), over 19 years, a twofold change in numbers of bears was observed. There was also a twofold fluctuation in litter size, the number of females with litters, and the percentage of young in the population also changed within these limits. When annual mortality of bears due to hunting outside the limits of the preserve equaled 11%, yearly growth exceeded it more than 2 times. This, as well as the small number of large animals, showed that a part of the population dispersed every year. At the same time, new individuals arrived which were previously not present. Locally populations in the mountains of the northeastern Caucasus (Nasimovich, 1940) have a nearly twofold fluctuation in the percentage of young (13–31%).

Field characteristics. The brown bear is very vigilant and cautious, and therefore is rarely seen by eye in forests on the plains. However, its presence may be known by many signs of its activity. This is first of all its feces and tracks, which are found on the surface of damp or wet soil, on wet moss, and on snow. Bear feces are extremely variable in color and consistency, depending upon the food eaten. In size, they may be compared only with feces of large domestic animals, but they are easily distinguished by the incomplete digestion of the plant food.

Prints of fore and hind paws are sharply differentiated: forefeet characteristically have prints with long strong claws, and also the width of the track is equal to or greater than its length. Greatest width of the track ranges from 9 to 19 cm. Tracks of the hind paws resemble tracks of bare feet of humans (claws are not always



452 Fig. 161. Track of right hind foot of same animal in Fig. 160, on shallow wet snow. Sketch by A.N. Formozov, about 2/3 natural size.



453 Fig. 162. Tracks of left fore and left hind feet of Tien Shan bear, *Ursus arctos isabellinus* Horsf., on wet clay. Aksu-Dzhabagly* preserve in Talassk Ala-Tau, 6 May, 1955. Sketch by A.N. Formozov after schematic of F.D. Shaposhnikov, about 1/2 natural size.

noticeable), but are sharply differentiated by the narrow heel and flat sole. Length of track of the hind paw ranges from 16 to 32 cm and width, from 8 to 14 cm.

Presence of the bear in the forest is also betrayed by rotting stumps and logs broken in its search for wood-boring ants; destroyed anthills and nests of terrestrial wasps (not to be confused with narrower and shallower holes of badgers); turf in forest openings rolled in a tube; excavated burrows of chipmunks; severed stems of umbelliferous plants (place of bite is ragged); trails proceeding through riparian or coastal tall vegetation beds in forest

*Misspelled "Dzhebogly" in Russian original—Sci. Ed.

openings and montane meadows; in autumn and spring, broken tips of young mountain ash and aspen trees: ragged bites on young trees; bark on trees stripped off by claws and deep claw tracks on stems (sometimes with traces of wool)—“bear marks” (P.Yu.).

Practical Significance

The commercial value of the brown bear is not great; in the 30's, 3–4 thousand skins were prepared annually. This figure does not reflect the actual quantity of the catch of the animals, since a considerable number of skins are retained by hunters for their personal requirements. In 24 districts of RSFSR (European part), out of 700 bears caught, the percentage kept was 60% (V.P. Teplov and S.G. Priklonskii).

The warm, but heavy, skin of the brown bear, with its coarse, thick dermis, is used only for preparing carpets, sleigh robes and rarely for travel coats. Bear fat is utilized by the food industry and is used for technical purposes. Its meat is also used as food, but not everywhere.

Representations of the damage brought about by brown bears to domestic livestock are greatly exaggerated. In a series of regions, where bears are especially numerous due to favorable conditions for their existence, it is just there the least harmful (Kamchatka, Altai, Caucasus); it feeds mainly on plant foods and almost never attacks livestock. But in those regions where loss of livestock to attacks by brown bears is observable, it is caused by only a few bears which develop, for one or another reason, the habit of attacking livestock. The majority of animals are completely harmless. Destruction of 1–2 of these predators completely stops similar cases, despite the large number of bears here. On the contrary, an unsystematic hunt of the first animal encountered and shot does not carry any kind of value.

Cases of attack by bears on humans are extremely rare. These cases are often observed when the person turned out to be between a female bear and her cubs, or an encounter with a wounded animal. Seriously emaciated, hungry “*shatun*” also attack humans; i.e. bears which do enter into hibernation in winter, not having accumulated sufficient quantities of fat, and sometimes also hungry bears (especially early in spring) disturbed at a fresh kill (Yurgenson, 1933, 1936, 1937, 1938; Teplov, 1953).

Needless to say, in a series of districts, hunting regulations wrongly place brown bears among the number of harmful animals which may be killed throughout the year. Carrion-bears most often attack livestock only, and especially those found in fenced pastures without herdsmen. In the taiga zone and locally in the middle [forest] zone, brown bears, in the course of a short period in milk stage
 455 of oat ripening, feed on them, trampling down more than they eat. This is not observed everywhere. Such cases were more frequent in the past, when individual peasants, farmers and forest-guards were sowing oats in small openings in the forest. There are a series of simple means for frightening bears from oats—hanging old clothes and rags in a circle around the field, stretching a string soaked in kerosene, going barefoot around in the field at night in the dew, and similar means. The oats bear is no more harmful to oats than domestic livestock allowed to escape by herdsmen. Sometimes, brown bears destroy forest beehives; such cases have caused losses in Byelorussia up to the present time (Serzhanin, 1955).

Brown bears are hunted with shotguns, lying in wait at night near a bait, or at the border of an oat field, often in a stand constructed in a tree, and also through accidental meetings. Traps for bears are less effective and are rarely employed. In montane regions, bears are spied out and ambushed during times they are grazing in the forest openings and alpine meadows. Winter hunting of bear is quite widely pursued—in the hibernaculum or by the chase. For hunting in dens, *laika* [dogs] are used. This is mainly an amateur hunting sport. Sometimes, *laikas* are used when hunting on black* trails in order to track, overtake and bring to bay the animal until the approach of the hunter. This method is not widespread due to the small number of *laikas* trained for this task. However, this method is the most suitable for destroying carrion-bears which attack livestock, since its use makes it possible to find a particular animal, which is necessary.

At the present time, hunting regulations of brown bear differ in the individual republics, and districts differ in an even greater patchwork often in no way justifiable. They often permit bear hunting throughout the course of the entire year, but this cannot be justified because it does not solve the problem of protection of domestic

*Not snow-covered—Sci. Ed.

livestock. In Krasnodarsk territory, hunting of brown bear is regulated by issuance of licenses. In Estonia, it is completely prohibited.

Taking into consideration the size of annual growth of the fully mature part of the bear population, the size of the annual catch must not exceed 10% of the total number. In 27 districts of the RSFSR, it was equal to about 35% (S.G. Priklonskii and V.P. Teplov) which must be considered excessive.

Brown bear may remain an object of tourist hunting, and of planned sport-hunting through license (P.Yu.).

Subgenus of Polar Bears

Subgenus *Thalarctos* Gray, 1825

POLAR BEAR, OSHKUI

Ursus (Thalarctos) maritimus Phipps, 1774

- 1774. *Ursus maritimus* Phipps. Voyage towards North Pole, p. 185. Spitsbergen.
- 1776. *Ursus marinus* Pallas. Reise durch verschiedene Provinzen d. Russ. Reiches, 3, p. 691. Laptev Sea.³⁴
- 1792. *Ursus polaris* Shaw. Museum Leverianum, 1, p. 7. Renaming of *marinus*.
- 1908. *Thalassarctos jenaensis* Knottnerus-Meyer. Sitzungsber. Ges. naturf. Freunde Berlin, p. 174. Iena Island, King Karl Land, Spitsbergen.
- 1908. *Thalassarctos spitzbergensis* Knottnerus-Meyer. Ibidem, p. 184. Seven Islands, Spitsbergen. (V.H.).

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Diagnosis

Dimensions large. Color monotone, white. Bare areas on lower surface of feet (callosities) very small and almost entire sole of foot densely covered with hairs. Facial portion of skull relatively long, but shorter than in brown bear. Last upper molar tooth small, narrow, not elongated, and only slightly larger than anterior; last lower molar small and considerably smaller than preceding tooth (V.H.).

³⁴Proposed here. See below "Note" in section "Geographic Variation"

Description

The polar bear is a massive animal, of heavy build on quite long, thick legs. Feet very large and broad, forefeet especially. Hind part of body massive and strong; stronger than fore part, which is relatively weak and seems to be laterally compressed (chest is not broad), withers lower than croup. Neck very long (relatively longer than in all other bears), very mobile, head relatively small, pointed, with narrow forehead and small rounded ears. They are smaller, and not so wide, as in brown bear; greater part of them hidden in fur.

Eyes small, dark; naked part of nose tip, as well as lips, black. Lips less free and mobile than in brown bear. Tail very short (relatively shorter than in brown bear) and completely hidden in fur.

- 457 Claws relatively small, smaller than in brown bear. Those on forefoot larger than on hind, and their length along the curve is 6.5–7.0 cm (digit III); length of claws on hind feet is 5.0–5.5 cm (digits I–IV). They are sharp, weakly curved, and pure black in color.

Lower surface of fore and hind feet thickly covered with hairs, except for very small bare areas (smaller than in all other bears). On forefoot, besides bare digital pads, there is a narrow transverse callosity, much narrower than in brown bear, in region of anterior part of metacarpal claws, and small rounded callosity on outer posterior part of foot. Position and form of naked areas essentially the same as in brown bear. On hind foot of polar bear, callosities are same as on forefoot, but outer posterior one is elongated or pear-shaped. Form and size of callosities are subject to certain individual variations. Moreover, in connection with shedding of fur (molt?), callosities are evident to different degrees (this is also true of animals in zoological gardens). Lower surface of feet between callosities covered with long hairs, which is characteristic of the described species. They entirely cover these callosities, and in this way, when the animal walks on snow and ice, it steps not on the bare callosities area, but on a thick hairy cushion.

The winter coat of adult animals is very dense and compact; however, it is relatively short, although hairs on posterior part of body are longer than on anterior. There are no long hairs on withers, and hair length in the shoulder region is all of 5–6 cm. On back, at croup, their length reaches 8–10 cm. Hair on lower part of sides and on belly greatly elongated (13–15 cm), also on rear side of hind



Fig. 163. Polar bear, *Ursus (Thalarctos) maritimus* Phipps. Sketch by A.N. Komarov.

leg (13–14 cm), and especially on rear side of forelimbs (16–26 cm). Very long, shaggy hairs (to 14.5 cm) outline the foot and protrude in the region of the digits, covering them almost completely. On bottom of foot, shorter, elastic hairs grow. Overall, fur on upper part of body, neck and head short and lying compactly, and on lower part of sides, belly and rear side of legs it is loose and shaggy. Hairs, especially on upper body, quite coarse and elastic, and on lower—flexible, depending mainly on their length. Overall, fur is coarser than in brown bear.

Summer, i.e. transitional, fur (one molt annually) shorter (on belly about 8 cm, on rear side of forelimbs, 10–11 cm, on croup—about 7 cm, etc.), but apparently, not sparse. Bear-cubs and young

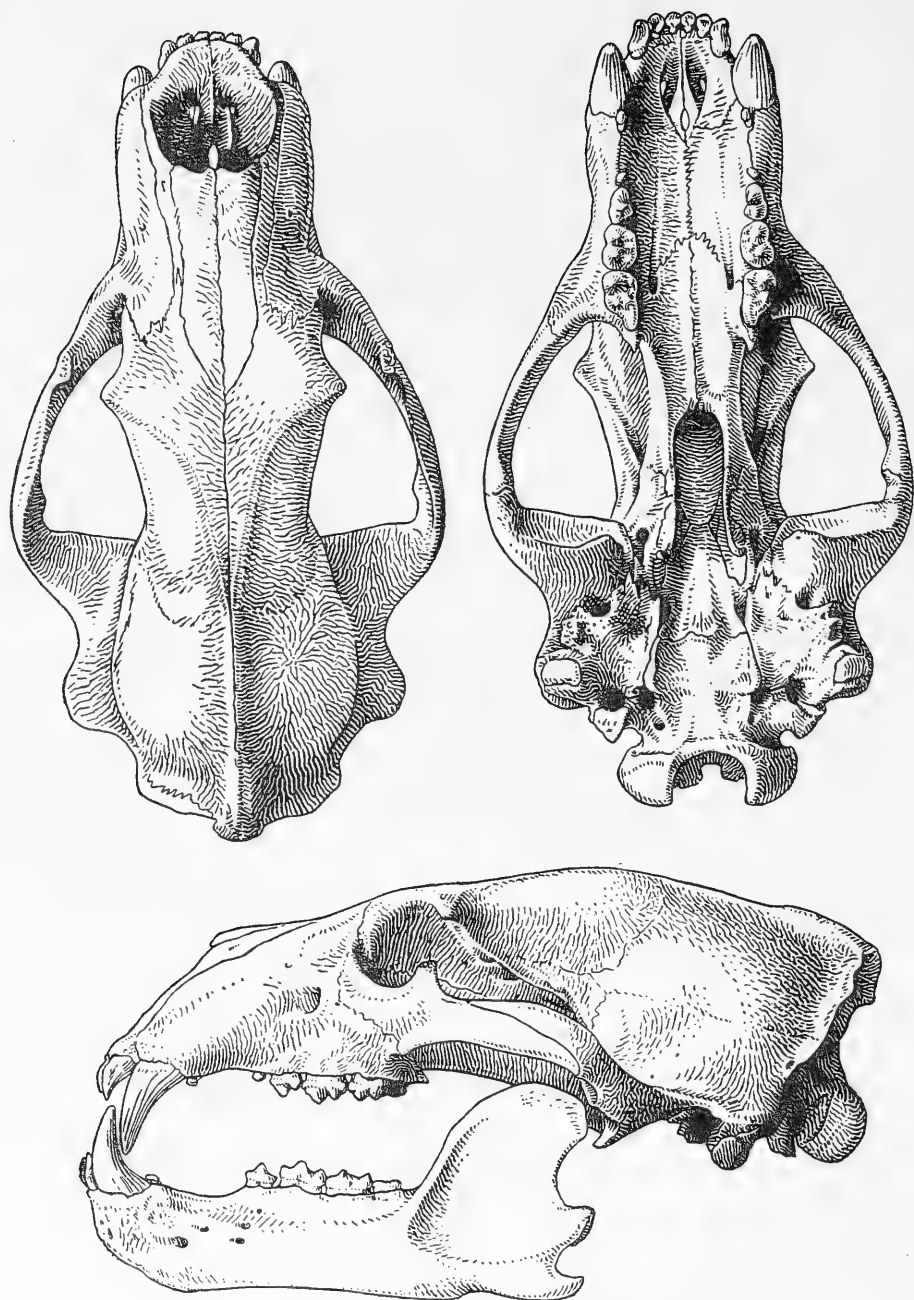
animals have relatively longer fur coat than old ones. Geographic variation in pelage is almost unexpressed.

Coloration is completely even on the whole body; white, sometimes pure white, often with slightly yellowish, sometimes strong golden-yellow tint; in extreme cases, giving animal almost a sulfur-yellow color.³⁵ Sex variation in color is absent. Color of young is usually purer white.

The skull of the polar bear is very similar to the skull of the brown, but differs from it in the following characters: 1) upper profile is straighter and projection of frontal region is not expressed or weak; 2) facial region is somewhat shortened, and the length of cranial region noticeably exceeds it: distance from anterior edge of premaxillae to line connecting ends of supraorbital processes is less, or, rarely, equal to distance from mentioned line to occipital crest, and distance from end of nasals to mentioned line is approximately two times less than distance from this line to end of occipital crest; 3) anterior part of muzzle is relatively wider: breadth of skull over canines is greater than its breadth across infraorbital foramen (in
459 brown bear, such a ratio may only be found in large Far Eastern bears—usually this ratio is reverse); 4) lower jaw is less massive, and anterior edge of the last molar lies slightly behind level of anterior border of orbit.

Canines are relatively strong, but molars are considerably smaller than in brown bear. Last upper molar only slightly larger than first; length of both molars is less than breadth of palate between first molars (Fig. 150); width between outer sides of occipital and articular processes greatly exceeds length of upper molars and last premolar of upper jaw (ratio is reverse in brown bear). Overall, by comparison to brown [bear], dental system of polar bear has a more “predatory structure”, in accordance with its mode of life and nutrition. It is characteristic that even in very old polar bears, the teeth are found in very good condition and are not at all affected by wear. In brown bears, strong interaction of the teeth occurs and wear begins very early; apparently, this is mainly related to the plant food of the brown bear, and in particular with soil that occurs on the teeth. Moreover, as may be judged from large series of museum skulls, the appearance of acute caries and diseases of the

³⁵These yellow tones of the fur disappear during the dressing of hide, and bear rugs always have a pure white color.



teeth, so frequently encountered in brown bears, sometimes with serious diseases of the lower jaw, are almost not found in polar bears.

Sexual variation is sharply manifested—the female skull is smaller than the male skull, sagittal crests in them are shorter and weaker, forehead is narrower, supraorbital processes consequently narrower, and zygomatic arches are weaker. The skull of the polar bear cub is similar to the skull of the brown, but differs by its narrower and more protracted rostral part, and its zygomatic arches are weaker and less developed.

Individual variation in the skull of the polar bear, both in dimensions and in structural peculiarities, is relatively insignificant and less by far than in brown [bear]. Overall, the polar bear is craniologically monotypic.

Although individual, especially large, races of brown bears are as large as the polar [bear], on the whole, the latter is larger than the brown. Maximal dimensions of polar bears are larger than the very largest brown bears, and they attain far greater weight. Moreover, in its geographic variation there is no sharp contrast, such as is found in brown (Kamchatka bear, *U. arctos piscator*, Syrian bear *U. arctos syriacus*), and there are no populations in which the types and range of individual variability are analogous to those of the Caucasian, *U. arctos meridionalis* or the East Siberian *U. arctos yeniseensis*. Individual variation of the polar bear is “normal”, but geographic variation is very small, which can be explained by the basic conditions of its life and the type of its geographical distribution area (see below).

Body length (without the tail) of adult males is 200–250 cm, rarely to 285 cm, reaching 302 cm³⁶ as an exception; body length of adult females is 160–250 cm; height at the shoulder is 130–140 cm, reaching 150 cm as an exception; tail length (with terminal hairs) is 20–22 cm.

Weight varies greatly, in part geographically, but chiefly in accordance with season and degree of fatness. Weight of very large males, in several parts of the range, is 700 kg and even 800 kg;

³⁶Information about a specimen 370 cm in length (Ivanov, 1933; after Tsalkin, 1936) does not merit confidence. This measurement often becomes exaggerated, because authors usually measure the animals with the tail and terminal tail hairs and sometimes the hide which is usually somewhat stretched.

there are data on bears weighing up to 1000 kg. Usually, weight is less. Females are always not only smaller, but also considerably lighter than males. Thus, males in eastern Greenland, in a status of normal nutrition, weigh 400–450 kg, well-nourished to 500 kg; females in this region, even very well-fed ones, here rarely are larger than 350–380 kg, i.e. their weight comprises about 75% of that of 460 males. Particularly large bears have up to 112 and even 180 and 192 kg of fat (last two figures are probably exaggerated).

Greatest length of skull of adult male is 353–412 mm, females, 324–360.5 mm; condylobasal length of male skull is 359–388 mm, females, 311–380 mm; zygomatic width of male is 187.5 to 274.5 mm, females, 194–199 mm; length of upper toothrow of males 110*–140 mm, females, 118–125 mm³⁷ (V.H.).

Systematic Position

The polar bear, in spite of its conspicuous external difference (color), represents a species extremely close to the brown [bear], *Ursus arctos* L. Only the American black bear stands closer to the brown bear, apparently, than the polar bear.

One may consider, apparently, that the polar bear is, in a certain sense, derived from the brown, further increasing the “predatory” trend (enlargement of canines, weakening of cheek tooth row) in the series of species of the family. At the same time, shortening of the facial portion of the skull, usual for the closely [related] species, and which is considered as characteristic of a certain sort of “primitiveness” (“infantilism”), here, apparently, does not have this significance and may be interpreted as a specialized character. It is, apparently, connected with weakening and shortening in the length of the toothrow. Moreover, the posterior region of the skull has by no means any kind of infantile characters (increased volume of braincase, basic weakness of crest development, etc.), and externally is typical of large forms of brown bear. In combination with other characters (coloration, dimensions, struc-

*In Russian original, “11”—Sci. Ed.

³⁷Measurements according to Hilzheimer 1930; Ognev, 1931; Birula, 1932; Palkin, 1936; Heptner, 1936; Anthony, 1928; Pedersen, 1945, Shereshevski and Petryaev, 1949. For additional data on measurements and their variation, see below in section “Geographic Variation.”

ture of limbs etc.), in the polar bear is manifested a well-defined complex of specialization for conditions in the Arctic, which is quite obviously derived from the brown bear type. It is characteristic that, having become an aquatic animal to a significant degree, in any event swimming well and often, the polar bear does not have the usual adaptations to the aquatic environment.

Palaeontological material, though not complete, also shows close relationship of the polar bear to the brown, and allows us to consider it as derived from the brown. Thus, the dental system of the polar bear of Eopleistocene time had greater similarity to that of the brown bear than has the contemporary [polar] bear (last premolar and second molar of upper [jaw]). In this way, the divergent evolution of the polar bear noticeably advanced even in post-Pleistocene time. Late Pleistocene *U. m. tyrannus* Kurt. was considerably larger than the present form (Thenius and Hofer, 1960; Kurten, 1964) (V.H.).

Geographic Distribution

Shores, islands and floating ice of the Arctic Ocean in the Old and New Worlds.

Geographic Range in the Soviet Union

The (reconstructed) range of the polar bear has a quite complicated structure. In it four differentiated regions can be traced: 1) the region of reproduction, by which is understood the territory where females in winter lie in dens and give birth; 2) the region of summer distribution of females and males of all ages; 3) region of winter distribution (migration) of males and barren female bears; 4) the region of long-distance movements to the south. With our store of knowledge, it is impossible to outline precisely each region separately.

462 The region of reproduction and the region of summer movements, generally speaking, are bounded on the south by the southern limits of the winter distribution region. In several places, the line of the southern border of all types are quite close together, in others they are quite distant from one another, often significantly. Here, the southern boundary of the range is taken by the line limiting the region of normal winter distribution of the animal. The region of movements is considered separately.

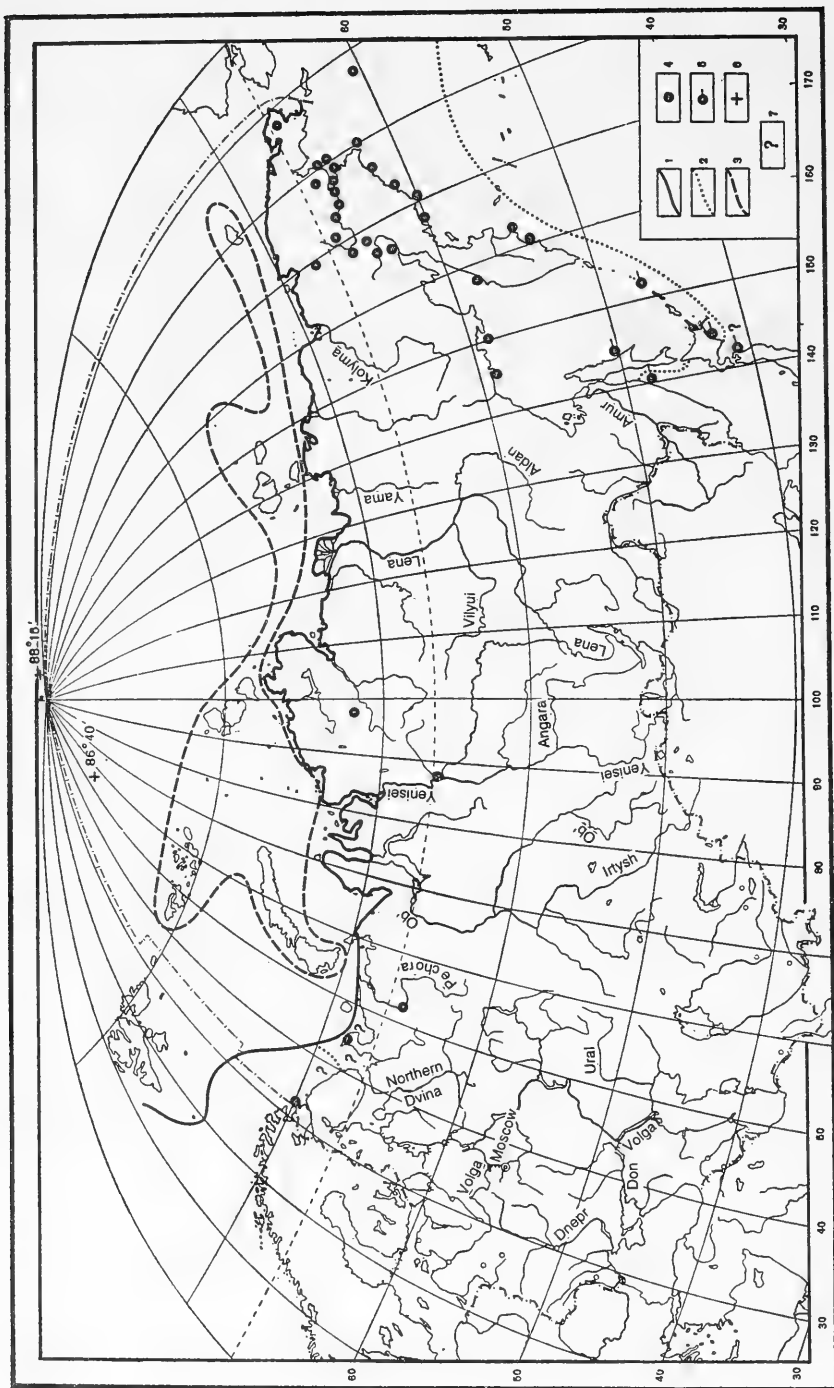


Fig. 165. Range of the polar bear, *Ursus (Thalartos) maritimus* Phipps., in the USSR (V.G. Heptner): 1—Southern boundary of reconstructed range, including region of normal migrations to the south; 2—Multi-year average of southern boundary of floating ice, where it does not coincide with southern boundary of range of bear; 3—Boundary of region where females give birth to young bears (islands); 4—Specific places of distant movements to the south beyond the boundaries of the normal range; 5—Poorly defined points of movements to the south ("Sakhalin", "Kuril islands", "Hokkaido"); 6—Several most northerly points where polar bears were observed in ice; 7—Possible places of occurrence in the west in ancient times and the doubtful extreme points of transgression to the east.

The southern (reconstructed) boundary of the range of the bear in the Barents Sea is closely connected with the distribution of floating ice. Its southern boundary includes the southwestern part of the sea from the north, northeast and east. It begins at the southwestern part of Spitsbergen, passes south around Medvezhii [Bear] Island, is again southeastward approximately to 45° E. Long., turns sharply to the southwest, reaching Svyat Nos in Murman (multi-year average). In this way, the range included in early times, Kanin, coastal tundras to the east of it (Timansk, Malozemel'sk, Bol'shezemel'sk), the northern part of the White Sea and, apparently, the easternmost part of the Murmansk coast.³⁸ However, there are few data on this part of the range.

In the beginning and middle of the past century, the boundary of the range, going on Medvezhii [Bear] Island, passed south of Kolguev and Vaigach, but, apparently, did not include Kanin, and probably, the coast of the mainland, except the Yugorsk Peninsula. Thence, the southern boundary went eastward, tracking the coast line right to the Bering Strait and to Provideniya Gulf. Beyond, the boundary crossed to Alaska through the Bering Sea (see below).

The entire Baidaratsk Bay was undoubtedly occupied; in the Ob', it was, apparently, distributed north of the Arctic circle, i.e. to the mouth of Ob'; in the Yenisei Gulf, they were known up to Gol'chikha and even to Tolsty Nos in the very mouth of the Yenisei at 70° N. Lat. North of this line, the range goes out to all the Arctic islands and floating ice, to the Pole itself. The most northern point of discovery is $86^{\circ}04'$ (Chapskii, 1946; there is information, not very well defined, on the occurrence of bears at $88^{\circ}15'$).

If, in winter time, the southern boundary of the range shifts maximally to the south (to the limits indicated above), then, as a rule, in the far north bears are not met with north of 80° N. Lat., occur there rarely, and do not penetrate far beyond this parallel. In summer, on the contrary, the southern boundary shifts somewhat to the north (very inconsiderably) but on the other hand, the range strongly widens in the Polar region, and it is at this time that the animals attain the Pole, i.e., they in fact live in the entire polar basin. In that way, there is a seasonal, and in part very strong displacement of the boundaries and of the whole range.

³⁸In exactly these regions polar bears were encountered by the people of Velikii Novgorod* ("ushkuiniks").

*Now Novgorod—Sci. Ed.

The region of reproduction (reconstructed) is considerably narrower than the general region of distribution and, within the borders of our country, occupies only the Arctic islands—Novaya Zemlya, Franz Josef Land, Severnaya Zemlya, New Siberian and Medvezhii islands and Wrangel' Island and small islands associated with them. This part of the range includes also the numerous small islands of the eastern and northwestern sectors and Kara Sea—in the regions of Pyasinsk Gulf, Khariton Laptev Coast, Nordenskjöld archipelago, Russkii and other more northern islands on the northern Taimyr—Komsomol'skaya Pravda (Samuil) coast, Feddei, and others. A great part of mainland coast of our Arctic area was not, apparently included in the region of reproduction (birth of young) of the bears—it includes only the extreme northern part of Taimyr, north of latitude 76° , and on the east of the peninsula from 76° N. Lat. to, probably, 74° N. Lat.*

At the present time, the boundary of the range has changed significantly. There have been no bears in Kolguev and Vaigach for a long time. In Novaya Zemlya, they are encountered along the western coast southwards to the Admiralty Peninsula (middle of
463 the northern island), along the eastern coast, and also in the northern half of Yuzhnyi [South] Island. Before the war, bears on Novaya Zemlya were considered very rare. During the war years, their number slightly increased, and the range, as related above, was restored (S.M. Uspenskii).

Along the southern coast of the Kara Sea as far as Dikson and somewhat farther to the east, the bear as a permanent inhabitant is absent, and it occurs only as a transient in the very easternmost part of the above-mentioned region. Already in the second half of the 20's at Dikson, and especially along the coast and islands of Pyasinsk Gulf, and even more on the Khariton Laptev coast, it was met with not only regularly in winter, but also in summer (V.G. Heptner). It is frequently, and more or less normally encountered, along the coast of northern Taimyr.

Along the coasts of the Laptev, East Siberian and Chukotsk seas, the animals are completely absent in a series of sections, or occur very rarely and accidentally. On the whole, it can be stated that the southern boundary of the range is shifted northward and bears at the present time are associated chiefly with the islands of the Arctic Ocean—Franz Josef Land, Novaya Zemlya, Severnaya Zemlya, New Siberian archipelago and Wrangel' Island and with

*Not shown on map, Fig. 165—Sci. Ed.

the small islands associated with them. This took place, not only due to the direct pursuit and killing of animals in connection with the opening up of the Arctic in all its sectors (see "Population"), beginning in the 20's, but also due to warming of the Arctic during the last 40 years, and particularly, 30 years. The shifting of the boundary to the north is also observed in North America and in Greenland, and climatic phenomena are also associated with this (S.M. Uspenskii). Some increase in the number of animals, which apparently took place in recent years in connection with its protection (see later) has not yet resulted in an increase (reestablishment) in range.

The region of reproduction, as regards its general outlines, at least during the last century, has changed little and at the present time, females den in almost all the area outlined above where it was previously noted, except, apparently, several islands in the eastern part of the Kara Sea. It is true that in Novaya Zemlya dens were almost absent before the war (except perhaps the most northern part on the Kara side); however, in the beginning of the 50's, females on Novaya Zemlya occupied dens, although they did not range as far as in the past. In the 50's, dens occurred along the Kara side of not only Severnyi [North] but also Yuzhnyi [South] islands (S.M. Uspenskii).

The main places of reproduction in our part of the Arctic are Wrangel' Island and Franz Josef Land. In each of these sectors, 150–200 female bears denned (S.M. Uspenskii, V.Ya. Parovshchikov). In our remaining places, the number of dens of pregnant female bears is less. For example, in Taimyr, there are, in all, about 20 to 30. On the whole, over the entire Arctic there are, apparently a total of up to 1000–1500 dens of pregnant females, of which the majority (by several estimates up to 2/3) of which are found in our above-mentioned region of reproduction (S.M. Uspenskii).

Irregular and accidental transgressions of individual animals to the south stretch out locally to very great distances beyond the southern boundary of normal occupation. At the same time, bears also appear deep into the mainland, far from the sea, but mainly on the sea coast. In the majority of cases, these transgressions are directly or indirectly connected with the transport of floating ice to the south, with which the animals are very closely connected in the summer time. They do not usually go beyond the limits of the

summer southern boundary of floating ice. Apparently, especially distant transgressions occur in years of maximum ice, when the ice is carried far beyond the limits of its multi-year average boundary.

Cases are known on European coasts of the appearance of bear in Finmark, in Varanger fiord, and at Kanin Nos. These cases are rare, occurring locally in the past [19th] and 18th centuries and were, undoubtedly, connected with extreme ice years. In such years of floating ice, the southern boundary of which lies in normal years
 464 far from the shores of Finmark and western Murman (see above), closely approach them. At Murman besides these [bears], appear several cold-loving northern species which usually do not occur here (Greenland seal, white whale; Heptner, 1930). Apparently, under these conditions, the bears appeared. At the present time, in connection with the extermination of the animal in the Barents Sea, bears no longer occur along the coasts of the northern extremity of Europe. Throughout the 20th century, it was apparently absent here.

Cases have been recorded of transgressions into the mainland on the Pechora from Ust'-Tsil'ma (about 320 km from the sea in a straight line), along the Yenisei to Turukhansk (more than 500 km from the sea on a straight line) and in Taimyr at the mouth and lower reaches of the Khatanga, along the Kheta and in its divide with the Dudypa (more than 300 km from the sea in a straight line; V.H. Skalon), along the Kolyma as far as the mouth of the Omolon, and others.

Along the Pacific coast, the animals were recorded in a series of places in Anadyr Gulf, in particular, in its westernmost part at the mouth of the Anadyr', at Cape Navarin, along the coast of Koryatsk Land (mouth of the Khatyrka, Shlyupochnaya Bay) at Cape Olyutorsk, in Olyutorsk Gulf (Apuka) and on the eastern shore of Kamchatka (Kronotsk peninsula, mouth of the Berezovaya in the southern part of Kronotsk Gulf). Farther to the south, wanderings are known to the Kuril islands, to the coast of Hokkaido, and even to Honshu (Hondo; information not fully defined). In the Okhotsk Sea, the polar bear is known to have been encountered on the western coast of Kamchatka (Tolbachik village in Mil'kovsk region), at Ol'skoe Island in Tauisk Gulf, near Okhotsk, on Sakhalin (indeterminate reference) and even in the extreme northern part of the Sea of Japan—at Mayacha anchorage near Sovetskaya Gavan'.

Accidental occurrence of animals on the Kuril islands and even

to the south in the Okhotsk Sea appears to be exceptionally rare, and is completely irregular. The same applies, apparently, to the eastern coast of Kamchatka. The appearance of bears in Koryatsk Land and especially in Anadyr territory, though rare, may be considered an entirely regular phenomenon. It is certain that, in previous times, at the time of large absolute numbers of animals in the north, it appeared here often.

Of great interest is the appearance of bears at the extreme east of Siberia, far from the seacoast, often at a distance of hundreds of kilometers from the ocean. These cases are, apparently, connected with animals wandering away from the ice to the Anadyr' and Koryat shores. Animals, drifting far to the south, after thawing of the ice, return to the north by a direct route, i.e., through the mainland. In a series of cases, the movement from the south to the north could be traced successfully and, apparently, the majority of movements were thus, although there are known cases where movement was towards Okhotsk Sea; i.e., to the south. Animals were encountered in a series of places along the Anadyr' from its mouth to Eropol (Utesiki, Ust'-Belaya, Il'muv'ya), Pokul'nya range (east of the upper Anadyr'), in the upper Penzhina and in Penzhina region, on the Chernaya river south of Markov on Anadyr', between the upper Kanchalan and Tashaina (south of the lower course of the Anadyr') and, lastly, in the upper Malyi Anyui.³⁹ All these points lie directly to the north of the region of vagrant bears wandering to the Anadyr' and Koryat coasts. It is possible that some bears move from the Okhotsk Sea through the Penzhinsk Gulf.

It is natural that in many cases bears are able to penetrate, and do penetrate, deep into the mainland, regardless of the indicated type of migration—for example along the Anadyr', to the south of Chaunsk Gulf, etc. The extreme northeastern part of the Chukotsk
466 Peninsula from the Arctic coast (Kolyuchinsk inlet and eastward) to the Bering Sea, the animals pass overland, apparently even often⁴⁰.

³⁹Range according to data of Pallas, 1776, 1811; Brandt, 1865; Middendorf, 1876; Pleske, 1887; Iokhel'son, 1898; Zhitkov, 1901, 1904; Buturlin, 1913; Sokol'nikov, 1927; Ognev, 1931; Adlerberg, 1935; Heptner, 1936; Portenko, 1941; Pedersen, 1945, 1957; Chapskii, 1946; Averin, 1948 and a series of other authors, and some unpublished data of S.M. Uspenskii.

⁴⁰The assumption that the described movement of bears through the mainland in northeast Siberia might itself be a track of a former transgressions of the sea, has no scientific foundation.

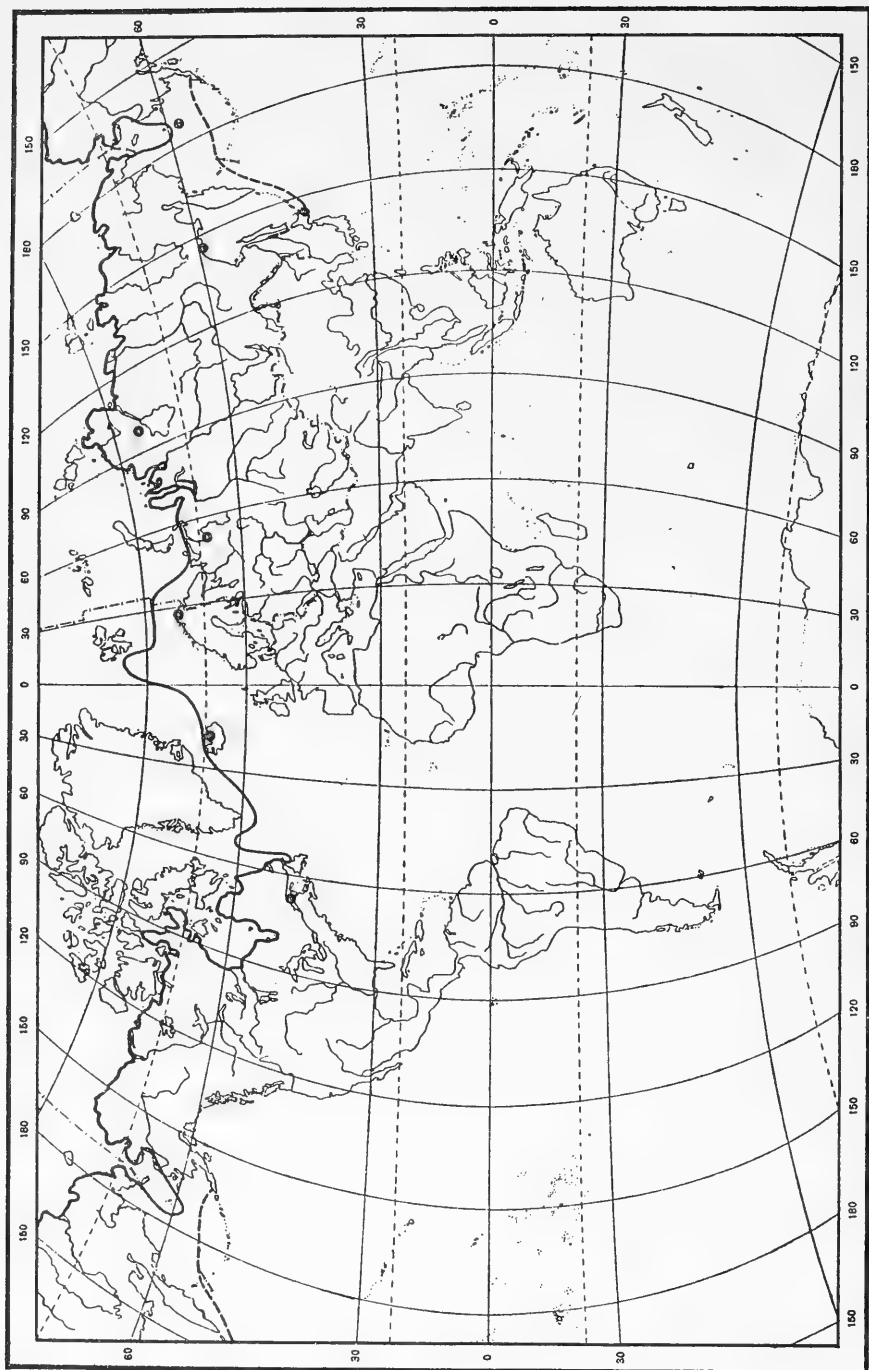


Fig. 166. Species range of the polar bear, *Ursus (Thalarctos) maritimus* Phipps. Solid line indicates the southern border of the range including the region of normal migrations and relatively short transgressions. Individual dots indicate several places of especially long movements; the broken line—the southern boundary of floating ice where it does not coincide with the boundary of the bears' range (V.G. Heptner).

Geographic Range outside the Soviet Union

In the Bering Sea, the range occupies its northern parts (Saint Lawrence, Saint Matthew, and Hall islands); on the mainland, the southern boundary passes along the northeastern and northern shore of the continent approximately from the mouth of the Yukon to the northern parts of Labrador. Transgressions, frequently together with floating ice, reach the Pribilof islands, and in the form of special rarities may perhaps reach the Aleutian Islands, penetrate far to the south along Hudson Bay, to its extreme southern part (mouth of Moose river; about $50^{\circ}45'$ N. Lat.). Together with floating ice, transgressions of the polar bear may penetrate far to the south along the eastern coast of Labrador—as far as northern Newfoundland and deep into the Gulf of Saint Lawrence (south; 49° N. Lat.).

The southern border of the range crosses over the floating ice of Davis Strait, to Greenland and the ice surrounding it, and with it, encircling the southern extremity of the island and to the ice of the Greenland and Norwegian seas, including Jan Mayen, Spitsbergen, and Medvezhii islands. Individual transgressions to the south reach the northern shore of the Iceland, Varanger fiord and North Cape (in the past). From this above-mentioned line, the range extends far to the north—in the same way as in the eastern sector of the Arctic. In Alaska, transgressions of bears are known deep into the continent, for 75 miles.

Within the range of the polar bear, differences in the distribution of places of reproduction (birth of young), winter and summer migrations, and the regions of seasonal distribution of the animals of various biological characters (mature males and barren females, pregnant females, etc.) are very specific. Only in the last decade (S.M. Uspenskii) were numerical irregularities in the distribution of the animal and their reasons clarified. The greatest number of polar bears are, apparently, connected with the so-called “Arctic ring of life”. It may be represented as a gigantic belt covering the central Arctic southward and is associated with the 200-meter isobath. Numerous, usually, large polynyas are associated with this ring, for example the Velikaya [Great] Siberian polynya—the most productive part of the high Arctic, in particular very rich in ringed seal [*Phoca hispida*—the main prey of bear. The life and range of the polar bear are associated, to a significant extent, with this “ring” (V.H.).

Geographic Variation

Geographic variation in the polar bear, which from time immemorial had been considered as one species, was first subjected to analysis in the 1900's* by Knottnerus-Meyer (1908). The level of work, following the worst traditions of Matchie, is astonishingly low—the author admits 6 species of polar bear, with 3 species for only East Greenland and Spitsbergen, described by him. The baselessness of this viewpoint is evident and was shown by several authors (Miller, 1912; Ognev, 1931; Birulya, 1932).

Geographic variation in the polar bear is insignificant. This is, apparently, explained by two factors—the comparatively small area of occurrence of the species⁴¹ and the considerable exchange of individuals between different populations. If females are, to some degree, restricted to definite sections of the Arctic, males roam very widely throughout the whole year, and violate the isolation of individual populations, which are generally relative under the geographical conditions of the Arctic. These wanderings pass both through the highest polar latitudes, and also, chiefly through the lower latitudes, apparently, where areas of free water (polynyas) or broken ice are found throughout the whole year (“Arctic ring of life”, see above).

467 There is an idea (Pedersen, 1945, 1956) that, in general, there is an uninterrupted regular movement of roaming bears in a more or less defined route from east to west around the whole Arctic in lower latitudes. This leads to total panmixia and completely excludes the possibility of formation of geographic races. This conception of migration and its routes, at least for our coastal sectors and central regions of the Arctic, apparently, requires some corrections. The point is that the movement of animals from east to west, which actually takes place, is determined not by any sort of active “over-flow” of the population by a clock-like pointer, but by the sum of movements (drift) of the Arctic ice which is, in the end carried to the Atlantic Ocean between Greenland and Spitsbergen. However, this “carousel” of the mass of Arctic ice

*In Russian original, “900-kh”—Sci. Ed.

⁴¹Conceptions about the dimensions of the range of the described species are usually exaggerated, since Mercator projection maps are most often used. Only polar or equal-area projections give a correct presentation.

is not so simple as it might seem from this very general discussion of the question. Nevertheless, the main idea deserves attention.

In spite of all, one must never lose sight of the fact that adult females are relatively sedentary—in winter, they are attached to their dens and places of reproduction (see above), and in summer they cannot, with their cubs, roam so widely as males. Their behavior to a certain extent neutralizes the wide movement of males.

It must also be taken into account that, as far as geographic differences are only manifested in general dimensions, the intensity of hunting apparently affects the characters of individual populations. Where animals are intensively pursued, the percentage of large individuals is, naturally, low. Therefore, the racial unity of the species is entirely probable. Nevertheless, to completely refute the known tendencies of geographic (population) variations and to ascribe the differences noted among separate groups on account of interference by humans is at the present moment still premature. That itself serves to indicate the presence of some sort of isolation of populations.

In our country, included in the borders of our sector of the Arctic, i.e., between approximately the 30° E. Long. and 170° W. Long. at least in the lower latitudes, two forms may be noted until there is a more thorough analysis of the whole question.

1. European polar bear. *U. (Th.) m. maritimus* Phipps, 1774 (Synonyms *polaris*, *jenaensis*, *spitzbergenensis*, *eogroenlandicus*, ? *marinus*).

Dimensions relatively small.

Body length of males in Franz Josef Land (48), 200–M 213–252 cm (most frequently between 200 and 210 cm); females (64) is 165–M 195–236 cm) most frequently between 190 and 200 cm).⁴² Body length of males from eastern Greenland (25), 199–M 221.4–

⁴²According to materials of Tsalkin (1936). The series of categories given by this author contain classes from 110 to 260 cm; i.e., they include young of the first year; averages are calculated according to this whole material (72 males and 77 females). Naturally, they do not reflect dimensions of animals of this race. Here, the material is recalculated, and for adults only, males starting with class 180–190 cm and females of class 160–170 were taken. For measurement of separate individuals, the midpoint of the class (185, 195 and so on) was taken.

229 cm; females (22), 160–M 169–189 cm.⁴³ Animals of this form from northwestern Taimyr usually have a body length not more than 230 cm (Heptner, 1936).

Maximum length of male skull, 353–M 355–377.5 mm; female, 334–335 mm; condylobasal length of male skull, 359–372 mm; zygomatic width of male, 187.5–M 223–241 mm, female, 194–198 mm; length of upper molars of males, 56–60 mm (Ognev, 1931).

Weight of adult males from eastern Greenland (normal nutrition) fluctuates between 400–450 kg, and particularly well-nourished males weigh up to 500 kg. Well-fed females have a weight of 350–380 kg (Pedersen, 1945).

468 Found in Franz Josef Land, Novaya Zemlya, the European coastline (in the past), Kara Sea, western coast of Taimyr (here is also the following form; see below) and corresponding sections of floating ice of the Arctic Ocean.

Outside the USSR—in Spitsbergen, eastern Greenland and the ice of the corresponding parts of the Arctic Ocean (for range boundaries of this form, see below).

For characteristics of this race, it is significant that very large specimens in Franz Josef Land and Spitsbergen occur extremely rarely—of 338 animals taken by different expeditions, only 2 were larger than 240 cm—one had a body length of 241 cm, and a “huge old male”, 252 cm. There is information about a specimen from Franz Josef Land (the method of measuring was not indicated) at 288.⁴⁴

2. Siberian polar bear. *U. (Th.) m. marinus* Pallas, 1776.

⁴³According to materials of Pedersen (1945). With respect to Greenland animals, the size (length) of the body is taken without the tail, as also in relation to specimens obtained from Franz Josef Land. Therefore, the means given differ from those given by Pederson (in the data given by him, the average length of the body is given including the tail and, apparently, even with the end hairs).

⁴⁴According to materials of Tsalkin (1936). Information about an animal at 370 cm is not believable (Ivanov, cited by Tsalkin, 1936). Data of Pedersen completely contradict the assertion of Payer that Greenland bears often have a body length of more than 300 cm (cited by Tsalkin, 1936). The data of Pedersen (1945) show that the idea concerning the large measurements of Greenland bears, compared to those obtained from Franz Josef Land, is incorrect, at least with respect to eastern Greenland. Their measurements are identical.

Individual, particularly large animals sometimes captured in eastern Greenland, Spitsbergen and Franz Josef Land are probably individuals of the Siberian race (mostly males) wandering from the east.

Dimensions larger.

Body length usually between 200 and 250 cm, but often nearer to latter figure. Separate individuals sometimes larger and attain 300 cm (without tail) and even a few centimeters more. Weight is between 400 and 700 kg; separate, particularly large, individuals reach 800 and even approach 1000 kg.⁴⁵

Skull larger. Greatest length of male skulls, 373–M 386–412 mm; females, 324–M 340–360.5 mm; condylobasal length of male skulls, 363–M 375–388 mm, females, 327.5–338.5 mm; zygomatic width of males, 217–M 239–274.5 mm, females, 194–199 mm; length of upper molars and last premolar of males, 57.6–M 61.7–64.0 mm, females, 50–61 mm (Ognev, 1931).

Zygomatic width is relatively larger than in *U. (T.) m. maritimus*, and zygomatic arches themselves somewhat more massive, frontal area abruptly ascends upwards, nasal region relatively longer, lower jaw more massive, and tooththrows slightly longer.

Found on Siberian coast, islands and floating ice from the longitude of western Taimyr to the Bering Strait.

Outside the USSR. Probably part of the American Arctic.

There exists vagueness concerning the ranges of both forms. Bears of the western Siberian northward (Ognev, 1931; Birulya, 1932) are usually assigned to the Siberian (eastern) form *marinus*, it sometimes being noted that animals of Novaya Zemlya possess features of a transitional character between this form and western *maritimus*. Together with this, there are data (Heptner, 1936) pointing to the fact that animals of West Siberia eastward to Taimyr are relatively smaller and they together with Novaya Zemlya animals are more correctly assigned to *U. (Th.) m. maritimus*. Thus, in western Taimyr, in the area between Dikson and the mouth of the
469 Pyasina lived a small bear (or lived in the 20's), which apparently

⁴⁵On the Komsomolskaya Pravda islands (Samuil; southeast of Cape Chelyuskin, at approximately 77° N. Lat. and 106° E. Long.), on 25 July 1935, an old male was killed with a body length of 285 cm (without tail) and weigh of about 1 metric ton (Shereshevskii, Petryaev, 1949).

Skull dimensions of this animal (Zoological Museum, Moscow University) slightly exceed even those of the previous animals; its greatest length—413 mm; condylobasal length—400 mm; zygomatic width—257.5 mm.

On the coast of northwestern Taimyr between Dikson island and the mouth of the Pyasina, an even larger bear was killed in the 20's, whose body length was 302 cm (without tail; Heptner, 1936).

belonged to the western form ("shore bear" of the native hunters with body length not more than 230 cm). In winter here, there appears the large form ("ocean bear") apparently the Siberian form *U. (T.) m. marinus*. The animals immigrate from the north-east.

Here there is a quite clear picture of the overlapping of ranges (for details, see Heptner, 1936). Therefore, the boundaries of the ranges of the two forms is not, apparently, found in the region of Novaya Zemlya, but in northwestern Taimyr. Precisely because of this limit, it follows that the nominal form must be accepted [in Novaya Zemlya], in spite of prevailing opinion. This is in full agreement with the fact, established by earlier authors, that the largest bears are encountered in Taimyr and eastward.

Generally speaking, the characters of both forms cannot be considered established and their independence is often doubted. Thus, Birulya (1932) saw that the difference between them lies only in the relative width of the zygomatic arches, and in the Siberian form, the wider and deeper frontal depression and more strongly developed processes.

Note. Pallas (1776, p. 691) described not a race, but a species of polar bear. The description was done by comparison with the brown bear, because before him, the polar bear was poorly known and unsatisfactorily described. The distribution was described as on the peninsulas and islands, and also on the pack ice of the northern Arctic Ocean, from which it nowhere moved away ("habitat in promontoriis insulis atque glacie fluctuante Oceani Hyperborei, a que nusquam recedit"). The first-hand material for description consisted of a young animal from the southern part of the Ob' Gulf, which was transported alive to Krasnoyarsk, where Pallas wintered with his student and fellow-traveler Vasilii Zuev (Pallas, 1776, p. 38). Therefore, in the latest literature, the type locality of the form *marinus* is correctly considered the Ob' Gulf.

At the same time, no one has made a direct comparison between Ob' bears (they have been absent for a long time) and the Spitsbergen bears. At that time, all authors, noting the large size of Siberian animals, referred [them] to animals from the shores of Middle and Eastern Siberia and the Far East. The above mentioned views show that bears of the western and southern parts of the Kara Sea do not differ from those of Spitsbergen. For the Ob' animals, it is certain, according to the query of Zuev, that Pallas (1776) referred to quite large measurements, though less than those

of eastern [bears]—up to 227–260 cm (converted from the Parisian feet which Pallas used—“septem et octo saepe pedes adulatorum magnitudo”).

Therefore, the name *marinus* is formally included in the synonyms of the nominal form, but the eastern bears must receive a new name. Until variation in our bears has been thoroughly revised, it is also undesirable, and it is proposed to retain the name *marinus* but to consider its type locality not Ob' Gulf but the Laptev Sea, where the large form undoubtedly occurs.

At present, it is difficult to give an opinion about the forms living outside the boundaries of our country, except for eastern Greenland (see above). All three subspecies described for the American Arctic—*groenlandicus* Birula, 1932; *ungavensis* Knottnerus-Meyer, 1908 and *labradorensis* Knottnerus-Meyer, 1908, were described from places lying near one another (western Greenland, Labrador and Ungava Gulf respectively), and are, apparently, identical. American authors usually assign bears of their Arctic areas to the nominal form (Hall and Kelson, 1959), although

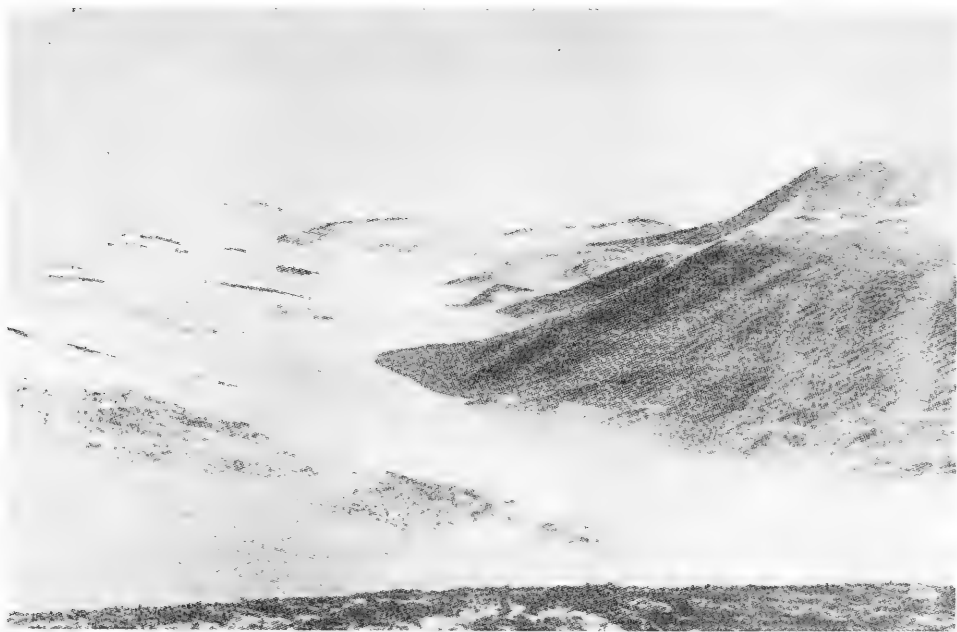


Fig. 167. Dresh-Kheb mountains—region of greatest concentration of bear dens on Wrangel' Island. Beginning of April 1964. Photograph by S.M. Uspenskii.

there are still some authors who even now recognize the "species" *labradorensis* (Anderson, 1946) and other "species" after Knottnerus-Meyer (Miller and Kellog, 1955). In the American Arctic, very large animals occur, but not inferior to North Siberian bears (condylobasal length of skull, 391 mm; Miller, 1912) (V.H.).

Biology

Population. Over a wide area of the Arctic Ocean the polar bear population is distributed unevenly. Their greatest concentration is observed in the region of confluence of the variously moving masses of sea ice. This region encircles the central Arctic, approximately
470 at the level of the 200 m isobath ("Arctic ring of life"; p. 693). The second region of concentration is at the edge of drifting ice, mainly near the Atlantic sector (Uspenskii, 1961). The population of polar bears is not stable: the animals periodically shift in different directions. Moreover, passive displacement, conditioned by continuous drift of sea ice from east to west in clockwise direction with a speed of about 2.3 miles per day, is of substantial importance (Pedersen, 1945; Uspenskii, 1961).

During the last 40–50 years the number of polar bears was strongly reduced as a result of their destruction. At the present time, according to various data (aerial count, den count, etc.), its total number was determined as 5–6 thousand head (Uspenskii, 1961). In the Soviet sector of the Arctic, their number hardly exceeds 2–3 thousand head.

Habitat. The polar bear is a marine animal. The main place of occurrence is floating ice of the Arctic Ocean, and to a lesser degree, the coastal zone of the sea-coast and its islands. The polar bear rarely moves on to the tundra, and usually not far but, sometimes, penetrates to the tree-line (along the Kolyma, 10 km above the mouth of the Omolon), usually in the period preceding their hibernation in dens, and in spring, when thaw-water lakes form on the ice, and cracks are still absent. On the tundra at that time it restricts itself to the valleys of creeks in ravines.

The existence of polar bears is closely connected with fissures, cracks, edges of ice floes and fast shore ice along the coast, because it is only here that they are able to catch their principal food—seals (ringed and bearded seals;* Rutilevskii, Popov and

**Phoca hispida*, *Erignathus barbatus*—Sci. Ed.

Shastin, 1939). Therefore, the southern boundary of the species range in Asia is limited to the northern coast of the continent, and in the Atlantic Ocean—the southern boundary of floating ice, and changes depending upon the position of the floe ice (Birulya, 1932). In Alaska, 1 bear traversed 32 square miles, with a range of 21 to 57 miles (observation from the air, Scott and others, 1959).

Food. The main food of bears is ringed seal, to a lesser degree, bearded seal. In the stomachs of 145 animals killed in Franz Josef
471 Land (Tsalkin, 1936), ringed seal was found in 67% of stomachs, walrus—in 14.4%, bearded seal—in 5%, vegetal mass—in 4% and birds—in 0.6%. Polar bears eat the carcasses of hunter-killed walrus (L. Popov, 1939), but themselves do not attack them because the adult walrus is a prey beyond its strength and the young ones are defended by the adults (Leonov, 1953). When bears and walruses meet, they pay no attention to each other (Rutilevskii, 1939). The bear hunts seals from ambush, waiting for them at their holes or cutting off their path to the water. The polar bear feeds most of all on ringed seals, mainly by virtue of their forming, in definite places, considerable accumulations (Pedersen, 1945). Ringed seals are subject to attack when resting or sleeping near air holes in ice. The most intensive hunting of ringed seals by polar bears occurs in spring and the beginning of summer, and at the time of molting, when the animals are less cautious; they employ a stalk using concealment (ice-hummocks) and hiding near the hole. Approaching to 4–5 meters, the polar bear makes a big jump. During an ambush, the bear waits until the head of the seal does not appear from the hole above the water* then, it strikes the seal's head with its paw and draws it to the edge of the ice-floe. The white bears very rarely encounter migrating seals—harp [*Phoca groenlandica*] and hooded [*Cystophora cristata*].

It usually eats the fat and skin. Only a hungry animal also eats the seal meat, leaving the bones. At the age of 6 months the cub-bear eats 2.5 kg of seal fat; the adult—6–8 kg (Rutilevskii, 1939), rarely more—up to 20 kg (Leonov, 1953). There is an opinion about its capacity to eat even 71 kg of walrus meat (Naumov and Lavrov, 1948), but this is an exaggeration. Polar bears do not themselves catch fish (Rutilevskii, 1939; Leonov, 1953). Hungry bears eat not only carcasses of seals and walruses, but even salted cod, carrion,

*Meaning unclear; perhaps the negative statement is a *lapsus*—Sci. Ed.

and also molting and nestling birds which fall from nests, and marine flotsam. There are known cases of their eating reindeer and Arctic foxes (Esipov and Pinegin, 1933). This accidental food occurs primarily in that period of hunger for the polar bear, when marine animals are not available. Depredation on stores of foodstuffs of the polar expeditions by polar bears is a common phenomenon.

Home range. Polar bears are extremely mobile, roaming widely, and have no permanent home range boundaries.

Burrows and shelters. The polar bear belongs among that group of animals that do not have permanent shelters. As they wander about the pack ice, they rest by lying among ice-hummocks. Obtaining its food within the limits of the coastal zone, the bear prefers to move to the sea-ice to lie down (L. Popov, 1939).

In winter, females, and in some cases males, construct dens in snow drifts. In Novaya Zemlya, such dens sometimes have 2–3 sections, including a “toilet”. In four investigated dens, only one chamber was found (Esipov and Pinegin, 1933). After construction of the den it usually covers them with snow, forming a large snow drift, in which a small opening sometimes remains, serving for breathing, but usually it is also blocked.

Dens of young bears are distinguished by careless construction and site selection. The den is usually oval inside, its length is 160–180 cm, and height 100–120 cm. Dimensions of the den, where the she-bear overwinters with cubs, reaches 260 cm. The length of the passage leading to the den chamber is 2.0–2.5 m, and even 3.0 m, rarely—10 m, and the diameter of the entrance is 60–70 cm (Pedersen, 1945).

On Pinegin Island, a den was found with a tight, dim corridor that was about 6 m long; the chamber was as high as a person and it had a diameter of about 3 m (Pinegin, 1933). On the pack ice, there are no dens; bears build them on the shores of the mainland and islands, frequently under over-hanging shorelines, among stones, rocks and so on, where large snow drifts are formed.

472 Dens are distributed primarily on the Arctic Ocean islands, but in part along the sea coast. In the eastern Arctic, this is mainly in the Franz Josef archipelago, Wrangel’ Island, and also the New Siberian islands. It is assumed that there are 1000–1500 dens in the entire Arctic. If we calculate that each is occupied by a pregnant female (with which not all investigators agree) and that the latter comprise about 20% of population, the total number in the popula-

tion is determined to be about 5000–6000 head (Uspenskii, 1961). In spring, when the litters have not yet emerged, perhaps a maximum of 8000 may be estimated.

Daily activity and behavior. The peculiarities of the light regime of the arctic do not facilitate the performance of a distinct rhythm of daily activity in the polar bear. Its life is closely connected with the sea and the pack ice; it is a true marine animal; it can swim and dive perfectly. The thick layer of fat and the dense



Fig. 168. Entrance of den recently abandoned by she-bear with cubs. Wrangel' Island. End of March, 1964. Photograph by S.M. Uspenskii.

fur permit the bear to remain in cold water for an extended time, and its strength and endurance in swimming are so great that it can swim for 10–20 and even 35 km. In the region of Wrangel' Island, the polar bear was observed in the open sea, 100 km from the edge of ice (N.N. Kondakov).

It swims at a speed of 5.5–6.5 km per hour. It can stay under water for 2 minutes. In and near water, it feels more confident and bold than on land, where it is not distinguished by its activity. It does not run quickly—its speed in an undisturbed pace is 4.0–4.5 km/h, that of males while fattening is up to 5.0 km/h. It trots 8–10–12 km/h, and in a gallop, up to 15 km/h, but such speed is possible only for a short distance. During quick movement, the polar bear quickly becomes exhausted. A human can tire a large polar bear after a distance of 10 to 15 km, because even after 5 km, its speed begins to decrease. However, in even large massive ice-hummocks, it maneuvers amazingly adroitly, and easily escapes from dogs and human. In so doing, the bear can jump across ridges of 1.5 to 2.0 m high and jump to a height [width ?] of 4–6 m (Rutilevskii, 1939).

The sense organs of the polar bear are well developed. It can see seal carcasses on the ice at 2–3 km. It can scent a strong odor (hot fat) at 6–7 km (with a fair wind). It hears the approach of a
473 human at 200 m (Rutilevskii, 1939). Where it is not pursued, it is bold and self-confident and exhibits great curiosity towards unknown objects. Polar bears attack man extremely rarely, even when hungry; an unexpected meeting with a female bear with her cubs is somewhat dangerous.

They tolerate a temperature of 10–15°C poorly, and seek shade (Kost'yan, 1954).

Hibernation and winter sleep. Information about the winter sleep of polar bears is quite contradictory. There are some indications that in Novaya Zemlya, males are active the entire winter (Esipov and Pinegin, 1939). This sometimes extends also to barren females and young bears (Lavrov and Naumov, 1948). The belief exists that only pregnant females, with few exceptions, retire to dens. They point out that old and strong bears are active in winter, whereas the younger hibernate for some time (Heptner, 1932). Among females the greater part hibernate in winter. A considerable portion of animals in the more southern regions, which are better supplied with food, do not den at all; those which do den,



Fig. 169. Polar bear running at a gallop. Wrangel' Island. Middle of April, 1964. Photograph by S.M. Uspenskii.

hibernate for a short time. Only a small portion of them hibernate from autumn through the whole winter.

Winter sleep of polar bears is related to food deficiency in winter, and to difficulty in obtaining it in the dark period of the year. Under more favorable conditions in the southern part of the range, where this period is shorter and it often happens that the sea is not frozen, sleep is shorter and the animals den more rarely. On the northern coast of Greenland, 90% of the animals den, in the northern part of Baffin Land—50%, and in southern Greenland—only 30%. On the whole throughout the range, 70–80% of the animals den (Pedersen, 1945).

Finally, there is information that all polar bears retire to dens, but for different periods: adult males den for 50–80 days, emerging from the den on the first days of February; non-pregnant females retire until 13–19 March, for a period of 115–125 days; females with cubs of the current year—until the first days of February for a period of about 160 days; and pregnant females retire to dens for 160–170 days, emerging from them at the end of April (Rutilevskii,

474 1939). In the region of Cape Chelyuskin, barren and pregnant females lie down to hibernate in the second half of November, as also do the cubs of the current year (Rutilevskii, 1939). Adult males retire later—by 12 December. On the eastern coast of Taimyr, a male was killed in a den on 9 December 1935 (L. Popov, 1939). Hibernation of males has been confirmed for the Olekma.

On the Olekma, emergence of bears from the den is noted in March–April. On Severnaya Zemlya, emergence from the den is extended, the principal mass emerging in the second half of March (L. Popov, 1939); on Novaya Zemlya, until the last days of April and even until the twentieth day of May (Pinegin and Esipov, 1939). On the whole, the time of retirement of bears coincides with the beginning of the dark period in the Arctic: in the south—this is the end, and in the north—the middle of November. The period of emergence is more prolonged—from the end of February to the second half of March and not later than the beginning of April. Old males are the first to den and the first to arouse (Pedersen, 1945). Delay in time of emergence of she-bears from the den is connected with delay in birth of the cubs.

Seasonal migrations and transgressions. Polar bears wander widely within the limits of the Arctic expanses they inhabit. Their migration is influenced by: 1) condition of the pack and 2) the distribution of seals (ringed and bearded seals), which depend upon the sea's ice cover conditions.

In summer, polar bears everywhere migrate to the north, and in winter—to the south. By winter, animals entering hibernation are concentrated on the islands of the Arctic Ocean (Severnaya Zemlya, Franz Josef Land, Wrangel' Island and north Novaya Zemlya) and in the coastal zone. On Bennet Island, in the period of mass migration of polar bears, tens, and up to 14 bears at one time may be seen daily passing from regions of solid ice to open water (Uspenski, 1961). On the eastern coast of Taimyr, polar bears arrive from the north, northwest and northeast in winter (L. Popov, 1939).

On Severnaya Zemlya, from May, when the ice is solid, they move out far from land from one [open water] lead to another, making a whole "bear highway" (Ushakov, 1951). If there is no [open] water, they move to the promontories and spits of land, where cracks and small leads, which attract ringed seals, are often found. With appearance of solid ice, they frequently move to fast shore ice, retreating southward.

Polar bears roam widely in the region of Cape Chelyuskin; the main direction of their movements is from east to west. There are also local and seasonal movements from north to south and back again. Those leaving from dens in spring to the west of Taimyr go to the east and north. Near the coast, in June–July, they migrate mainly to the west, where marine animals are concentrated (Rutilevskii, 1939). Animals appear in the northeastern part of the Kara Sea in the first half of winter, migrating from nearby regions. In the middle of winter large bears appear, arriving from the remote parts of the Arctic Ocean. With the approach of spring, they gradually migrate again to the northeast along the coastal fast shore ice. Bears already adjacent to places remain for a longer time and the last of them depart in June (Heptner, 1932).

In Spitsbergen, polar bears migrate following the southern limits of the pack ice, near which seals are found; they constantly move between Spitsbergen and Novaya Zemlya, appearing periodically on Medvezhii [Bear] Island. To the north, they go as far as the region of the pole, occurring both on solid and on broken ice (Birulya, 1932).

Cases are known of drifting of polar bears on fields of pack ice far to the south—to St. Matthew Island in the Bering Sea (Sokol'nikov, 1927), and the Okhotsk coast (G.D. Dul'keit). During migrations, they sometimes accomplish long traverses (10 km and more) of tundra (Sokol'nikov, 1927) (for details, see section on "Geographic Distribution").

Reproduction. On Novaya Zemlya, rut commences in March (Esipov and Pinegin, 1933), but there is some indication (Dubrovskii, 475 1937) that it is prolonged here from April to August. On Severnaya Zemlya, it is observed from the middle of June to July (L. Popov, 1939). In the region of Cape Chelyuskin, the males and females were observed to stay together from 2 July to 27 August (Rutilevskii, 1939).

Outside the boundaries of the USSR, the breeding period* occurs from the end of March or beginning of April to the end of that month. In the absence of conception, there is a second, late, estrus in May. Estrus in females lasts 3 weeks and is usually repeated every 3 years (Pedersen, 1945)—according to other data, every

*Misspelled "perid" in Russian original—Sci. Ed.

other year, but in the absence of conception, even earlier (Kost'yan, 1954).

Usually, 3 to 4 males go after a female who comes into estrus. Therefore, it is supposed that the ratio of sexes equals 3 to 1; however, up to 7 males, moving at considerable distances from each other, have been observed with one female (Pedersen, 1945). If estrus in females actually occurs every 3 years, then approximately 1/3 of the adult females are found in estrus each year, and the presence of several males near the female is fully understandable.

In the Leningrad Zoo, the period of rut proceeds annually from 15 March until the end of April (Kost'yan, 1954). If copulation takes place in July or August, the female remains barren. Copulation in the period of rut is repeated many times. The duration of pregnancy ranges between limits of 230–250 days, i.e., about 8 months.

The behavior of the pregnant females changes noticeably by at least October, when they turn towards the nearest land. This is especially noted where bears are far away in the open sea. Besides large mountainous islands, pregnant females occupy dens on small "bear" islands. Such females often build snow-burrow dens not on the coast, but several kilometers from it. The den is constructed from the end of October—beginning of November, and is occupied from the middle of November, when embryos development begins after the latent phase.* Embryos were never found in females killed outside of dens (Pedersen, 1945).

On Novaya Zemlya, according to various data, birth of the young takes place in January–April (Dubrovski, 1937), [or] in December–January; on Krestova Bay, in March–April (Esipov and Pinegin, 1939), and beyond the borders of the USSR (Pedersen, 1945), during January. In the region of Cape Chelyuskin, parturition is observed in January–February, sometimes later (Rutilevskii, 1939). On Severnaya Zemlya, birth of young occurs in the middle of June and even in July (Popov, 1939). Although in the polar bear, as in species with a latent stage in embryonic development, the time of birth may be shifted significantly due to variation in the duration of this stage, claims of June–July are undoubtedly in error. In general, one may state that the time of birth occurs in the middle and second

*Delayed implantation—Sci. Ed.

half of winter. In the Leningrad Zoo, birth of young in polar bears took place from 10 November to 28 December (13 cases).

The number of the young bears in a litter equaled two in 11 cases, and one in 2 cases (Kost'yan, 1954). Under natural conditions, the number of young varies from one to four. Of 27 cases (different authors), the litter contained 2 cubs in 16 cases, and in 10 cases—one, and in one—4 (Pedersen, 1945). The cubs remain with the female bear about 1–1/2 years.

Growth, development and molt. Bear-cubs are born helpless and blind, with closed ear openings. Wool is sparse and short, and skin pigment is absent. On the 3rd day after birth, body length is 28–32 cm, average weight—about 755 g (650–840 g). On the 26th day, body length increases inconsiderably—to 35–38 cm, but weight grows to 1125–1275 g. Pigmentation [of skin] is completed by the end of the first month. Eyes open on the 30th–31st days; at that time the ear openings also appear. They begin to crawl at the age of 45 days. The first signs of the appearance of sense of smell are



476 Fig. 170. Bear-cubs which have just emerged from the den. Wrangel Island. 15 April 1964. Photograph by S.M. Uspenskii.

observed at the age of 50 days. Teeth are cut at the end of the 2nd month. At this time, the cubs regularly crawl out of the den, but are
 476 capable of short walks with their mother not earlier than 3 months after birth. They feed on the mother's milk for 6–8 months (Kost'yan, 1954). In individual cases, they suckle the mother up to 15–18 months (Rutilevskii, 1939).

At the age of 60 days, males weigh about 7 kg, females about 6 kg, with body length of the former 58–60 cm, of the latter, 54–58 cm.

At an age of 4 months, cubs have attained a weight of 22–23 kg; at 6 months of age with length of about 110 cm—40–43 kg, and at 8 months—58–62 kg. Body length from the age of 6 to 9 months increases by 6–7 cm per month. At the time of winter sleep, growth almost ceases. They begin to swim at the age of six months. Replacement of teeth by permanent ones is completed by the 10th–11th month; at the conclusion canines are replaced by October (Rutilevskii, 1939). Sexual maturity is attained in zoos at 5 years (Kost'yan, 1954). In Greenland, the females participate in reproduction at 4 years, and the males—8 years (Pedersen, 1954).

In contrast to males, females with cubs restrict themselves to coastal areas, and do not move far, either into the tundra or the sea. Yearling cubs abandon by the mother subsequently stay together for about 7 months.

The she-bear leaves the den at the end of March—beginning of April, rarely earlier, when the cubs are 8 to 9 weeks old. Sometimes for several days thereafter, she remains near the den, and then goes out to the coast near sea ice. At first, she sometimes leaves the cubs in a den. While hunting seals, the she-bear leaves the bear-cubs in a secure place, but never on the mainland, or else they accompany her.

Adult males are a danger to the cubs, and she-bears avoid them in every way. They also, though very rarely, move to islands and the sea coast. Usually, the cubs spend the first winter in a den with the she-bear, who leaves them at the end of their second year of life, when they are equal to her in size. However, the cubs sometimes spend a second winter with the she-bear and go with her in spring to hunt seals (Pedersen, 1945).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Except for humans, the polar bear has no enemies. In the Arctic, the polar bear also has no competitors for

477 their main food—seals. On land, dogs and wolves are enemies of the polar bear (Pedersen, 1945). In water, it is walrus which it fears most of all, and the killer whale (*Orcinus orca*).

Diseases which markedly influence changes in numbers are not known.

There are no data on mortality, but it may be assumed that cubs naturally die from starvation, being carried away on pack ice, and others like it in magnitude. Death of adult bears is determined by their economic use by humans, starvation and other accidental causes (carried away on pack ice, etc.). Natural mortality among adults is probably not high. During the last decades, trichinellosis was very widely spread among polar bears (S.M. Uspenskii).

Field characteristics. It is impossible to confuse the polar bear with any other animal in the polar regions of the Arctic.

Its tracks are distinguished by the marks of the powerful claws on the forelimbs. In contrast to the brown and white-chested

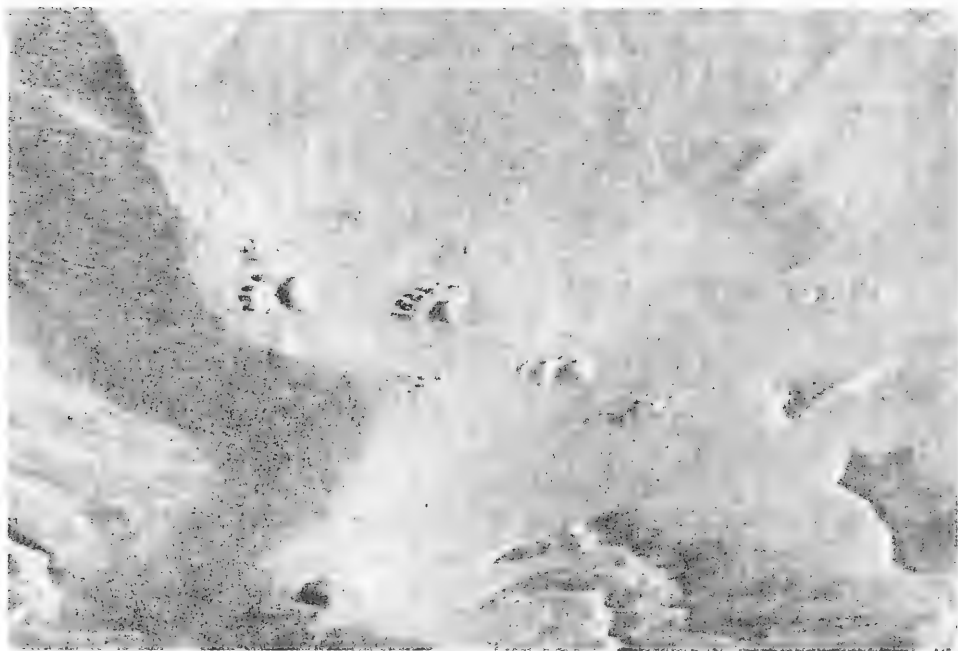


Fig. 171. Tracks of a she-bear and cubs traveling from Wrangel' Island to the ice. Middle of April, 1964. Photograph S.M. Uspenskii.

(Himalayan) bears, the lower surface of the feet of the polar bear is covered with wool. Therefore, the large, broad and flat track of its hind limbs are more similar to those of the track of a human foot shod in fur shoes, than to the print of his bare foot, which is characteristic for the brown bear (P.Yu.).

Practical Significance

The skin of the polar bear has limited use, and is principally used for decorative purposes (carpets). There is no exact information on the number of polar bears obtained in the Soviet sector of the Arctic before the prohibition of their taking in 1956, although it is calculated to be in the hundreds of animals. The yearly take of polar bears in the entire Arctic in 1957–1958 was determined to be 950–1400 individuals, of these 100–200 in Alaska 400–500 in Canada, 478 150–200 in Greenland, 150–300 in Norway, and in the USSR, presumably 150–200 (Scott et al., 1959). The main significance of this animal lies in the fact that it serves as an emergency stock of meat and fat for the members of Arctic expeditions wintering in polar stations and so on. Only in these events and in cases of direct danger to life, is the killing of polar bears permitted.

Hunting takes place on the ice by rifled weapons, ambush, stalking and driving, sometimes with the help of dogs. There also exists another method of hunting polar bear from specially constructed, baited blinds.

As early as 1954, foreign organizations for nature protection have raised the question of the necessity of complete protection of this animal in all sectors of the Arctic, and in this sense have applied measures.

In the USSR, by decree of the government, hunting of polar bear has been prohibited since 1954. Only in emergency conditions is it permitted to expeditions and overwintering people at polar radio-stations. Hunting of polar bear (and snow goose) on Wrangel' Island, the main concentration area of the dens of pregnant she-bears was declared illegal. All these measures have helped to prevent the extermination of the polar bear; however, convincing data about growth of their numbers are still absent. The fate of this animal still fills us with apprehension, especially as a certain number of bears are known to be killed yearly under the pretence of self-defense and for capturing cubs for zoos.

Counting from the air in Alaska in the late 50's showed some increase (1956—1 animal per 148 km route, 1957—1 animal per 56 km, 1958—1 animal per 55 km; Scott et al., 1959), although these indications may be based upon accidental causes (P.Yu.).

Subgenus of the White-chested Bears

Subgenus *Selenarctos* Heude 1901

WHITE-CHESTED, BLACK BEAR⁴⁶

Ursus (Selenarctos) thibetanus G. Cuvier, 1823

1823. *Ursus thibetanus* G. Cuvier, Rech. ossement fossiles, 4, p. 325. Assam.
 1841. *Ursus torquatus* Wagner, Schreber* Säugethiere, 2, p. 144. Renaming of *thibetanus*.
 1901. *Selenarctos ussuricus* Heude, Mém. Hist. Nat. Emp. Chin., 5, pt. 1, p. 2, pl. 11, fig. 10. Ussuri Territory (V.H.).

Diagnosis

Size moderate. Coloration black, very constant; on chest, a large white spot. Lower surface of forefeet bare (covered by one continuous callosity). Facial part of skull relatively short, cranial part large, broadened; sagittal crest weakly developed, last upper molar wide and long, considerably larger (almost twice) anterior, last lower molar small, not narrower posteriorly (V.H.).

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Description

In general appearance, the white-chested bear is similar to the brown bear, but its build is lighter—the body is not so massive, and limbs are thinner, taller and slender. In contrast to the polar bear, the anterior part of the body is more powerful than the

⁴⁶The present, very apt, native name for this species in the Far East—white-chested bear (Bromlei, 1956). The second name is pedantic. In the literature, this species is called also the Himalayan and Tibetan bear. It is not necessary to retain this artificial nomenclature, the more so since the latter gives a false impression about the range of the species.

*Misspelled Shreber in Russian original—Sci. Ed.

posterior, and the hind limbs are weaker than the forelimbs.⁴⁷ In motion, the white-chested bear looks as if its hind legs are crossed with its short legs under its body. The main feature mentioned about the build of this bear is more pronounced due to the fact that it has high withers with long hairs, and when moving, its neck and head hangs down low. The head is relatively small, and quite narrow, with an elongated muzzle. The ears are very large and broad, narrow at base and strongly protrude from the fur, giving the animal a unique appearance.

The lips and nose are very mobile, and larger than those of the brown bear. The tail is short and hidden in the fur. The claws are large, and more abruptly curved as compared to black* bear; claws of the hind limbs are relatively longer than in the brown bear; and differ slightly in length from the forelimbs (ratio of length of anterior to posterior is 1.17 : 1.00 against 1.74 : 1.00 in the brown bear). The claw color is black.

The hind sole has 5 well developed bare digital pads (callosities), the base of the free part of the digits being covered with hair; the remaining lower surface of the sole is bare, as in the brown bear. On the forelimbs, not only are the digital pads bare, but also the entire lower surface of the foot.

Fur is dense, fairly long and fluffy. Hair length on the back reaches 100–105 mm; on the withers, occiput and neck is even longer and along the sides of the neck reaches 160 mm. In the thoracic region and abdomen, the hair is, on the contrary, short and has an overall length of about 20 mm (in the brown bear, it is very long in these regions—200–205 mm). In winter coat, underfur is well developed; in summer, it is absent, and the fur is shorter.

Coloration of the winter coat is very beautiful, brilliantly black, with unique reddish brown highlights on the head and the thick underfur, and sometimes on the sacrum. In summer, when the

⁴⁷The ratio of the weight of the disarticulated anterior extremity to the weight of the posterior in the white-chested bear is 1.1 : 1.0, in the brown bear, 1.0 : 1.05 (average of 6 specimens; Bromlei, 1956). An individual taken on 5 August 1940, the weight of the two hind limbs, disarticulated at the trochanteric joint, comprised 9 kg; the two fore limbs together with shoulder blade was 10.6 kg. The forelimbs are so strong that an animal with broken hind limbs can move on its fore limbs and even climb a tree with, knots though not high (G.F. Bromlei).

*Meaning not clear; may refer to brown bear, or to American black bear—Sci. Ed.



Fig. 172. White-chested, or black bear, *Ursus (Selenarctos) thibetanus* G.
Cuv. Sketch by A.N. Komarov.

undercoat disappears, the coloration is pure black. On the thorax, a large, almost always sharply outlined light patch is found. Its
480 outline is quite variable, but it always elongated in a transverse direction and generally has a half-moon or crescent form, with the ends of the "crescent" directed forward; sometimes from the middle part the projection of white coloration is directed backwards.

Occasionally, the patch has an oval form, or is divided into two (a larger part lying above, and a small—below) or even into three. In rare cases, the patch may be completely absent. In our bears the patch is most often in the form of an angle ("izhitsei")*. A white patch is sometimes situated on the lower lip and chin. The color of the patch is usually pure white, sometimes with a more or less ochereous film. There is no sexual difference in color, and the individual variation, not counting the white patch, is negligible.

The skull is relatively small but massive, with massive lower jaw. In contrast to the other two species of the genus, projections

*Name of a V-shaped archaic letter in Cyrillic alphabet—Sci. Ed.

and crests of the skull are weakly developed. The sagittal crest is low and short, even in old individuals, and is only noticeable on the posterior part of the parietals; it never extends beyond their anterior edge. Its length does not exceed 19–20% of skull length (in the brown bear, it may comprise up to 41%). From the sagittal crest, two arciform flattened ridges (crests) extend forward, reaching the supraorbital processes. In this manner, the frontal area, which in other species has a rhomboid form, in the white-chested bear extends backwards as a long projection to the parietal bones.

The general profile of the skull is a gently sloping arch, and a frontal projection is not formed. The frontal area is neither impressed nor flattened, its transverse profile being slightly convex. The supraorbital processes are relatively weak (weaker than in other bears) and depressed (not elevated). The occipital crest is well developed, its ventro-lateral part particularly large and broad, so that the whole posterior part of the skull is broad. The zygomatic arches are quite weak, but in the posterior part, in accordance with the size of the braincase, they are widely separated. Their posterior part, in the region of articulation with the lower jaw, is greatly flattened and broadened transversely.

One of the main characteristic features of the general skull structure includes the strong shortening of the facial part of the skull, and the broad and voluminous posterior expansion of the braincase. The latter feature is emphasized by the structure of the occipital crest indicated above. In combination with the weak development of the crest and the general sculpture of the skull, and the almost undefined postorbital constriction of the cranium, this confers on the skull of the described species an infantile appearance.

The distance between the anterior end of the premaxillary bone to the line uniting the ends of the supraorbital processes is considerably shorter than the distance from this line the end of the sagittal crest (or the mid-point of the occipital crest). The distance from the anterior edge of the orbit to the anterior point of the premaxillary bone is less than the distance between the ends of the supraorbital processes. The muzzle is relatively broad, its width above the canines is equal to the width between the infraorbital foramina or even exceeds it. In concordance with the general shortening of the facial part of the skull, the lower jaw is also shortened.

The toothrows, compared to those of the brown bear, are relatively short (comprising about 40–41% of the total length of the skull), the canine is strong, and the other teeth are, in relation, somewhat weaker. On the whole, the dental formula is the same as that of the brown bear; in particular, the last upper molar is particularly large. Compared to it [brown bear], however, [this molar] is slightly smaller—its size is somewhat less than twice the length of the first molar. The last lower molar is small and is much smaller than in the brown bear. It has a rounded-rectangular or oval form, usually without the constriction in the posterior part characteristic of the brown bear (Fig. 150). The cusps on the surface of the
 482 molars are more weakly developed than in the brown bear. The first three premolars, which often fall out with age in the brown bear, are usually retained.

Dimensions are considerably less than in our other bears, and correspond approximately to the dimensions of small races and the individual variants of the brown bear (Table 47).

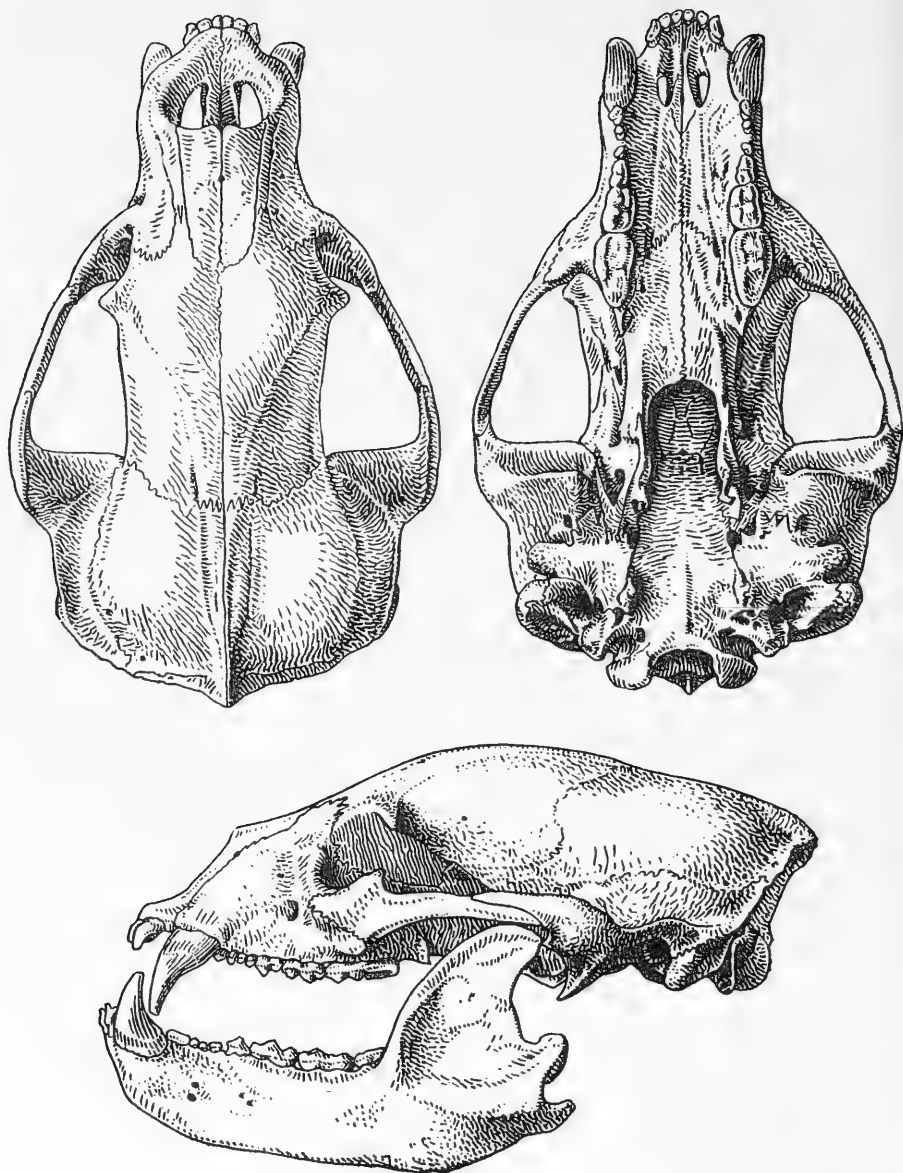
Large males have a size [body length] of about 150 cm;* occasionally including bears with body length of more than 170 cm, and very rarely those of 200 cm.⁴⁸ The greatest weight of the bear is in autumn, especially in years of good food harvest, when they put on much fat before hibernation.

Table 47. Dimensions of animals (in the flesh) from southern part of Ussuri territory (Tachin-Chtan range) (Bromlei, 1956)

Specimen	Body length	Tail length	Ear length	Chest circumference	Height at withers	Weight in kg
Males						
6 January	168	10	13	134	65	117
18 February	153	9	15	74	87	110
9 November	171	11	12	125	86	147
Females						
30 October	128	7	12	102	64	65
24 November	135	7	15	95	82	80
12 May	144	10	18	89	79	69

*Contradicts Table 47, where mean body length is 164 cm—Sci. Ed.

⁴⁸On 3 December 1940, Yu.A. Salmin killed a male in Terneisk region with a body length of 197 cm (G.F. Bromlei).



481 Fig. 173. Skull of the white-chested bear, *Ursus (Selenarctos) thibetanus*
G. Cuv.

Greatest length of skull of males (10), 295–M 311.7–328 mm; condylobasal length of skull of males (10), 271–M 291.6–315 mm, of females—260–268 mm; zygomatic width of skull of males (9), 185–M 199.5–228 mm, of females—163–173 mm; length of upper toothrow in males, 110–112 mm, of females—98–100 mm (from materials in Zoological Museum, Moscow University and the data of Ognev, 1936).

Females are always somewhat smaller than males. Individual variation is not great, and has a “normal” character. There is nothing of the kind of variation that occurs in some brown bear populations. Geographic variation in the size exists, but is generally small and, in the majority of cases, less than that in the brown bear. It is not pronounced within the boundaries of our country.

Systematic Position

The white-chested bear must, obviously, be considered a more specialized form than the brown bear. In this respect, it is analogous to the polar bear, although as regards its own degree of difference, it stands farther from the brown bear than does the polar bear.

Moreover, specialization of the white-chested bear has a completely different, so to say contrary, direction as compared to the polar bear. As was mentioned above, the polar bear is an entirely terrestrial* animal, a good swimmer, and a true predator. The white-chested bear is an herbivore to a greater degree than the brown [bear], in whose structure may be observed completely evident features of adaptation to tree-climbing (development of the fore limbs and claws, short fur on the chest and abdomen etc.). In
483 Ussuri territory, this species spends up to 15% of its time in trees, feeds there, and hibernates in hollows. The brown bear can also climb trees, but only up to the second year of age (Bromlei, 1956).

Biologically, but also morphologically, the white-chested bear itself represents the beginning of that line of specialization which is maximally attained in the South-Asian arboreal forms—the sloth (*Melursus ursinus*) and Malayan (*Helarctos malayanus*) bears.

*In the sense that it does not climb trees; as noted above, it is primarily marine—Sci. Ed.

In systematic relationships, however, it apparently has less in common with the sloth bear; but (attention was not drawn to this point) its skull has common features with the skull of the black Malayan bear. This similarity is more obvious when compared with the skull of a young Malayan bear.

The skull of the adult animal [of *Helarctos*] differs strongly, but some of its characteristic peculiarities themselves represent the same features of the white-chested bear, but in hypertrophied form (still greater shortening in the facial parts, and broadening of the zygomatic arches posteriorly, posterior broadening of the braincase, mainly at the expense of the occipital crest, the further reduction of tubercles, crests etc. of the skull, etc.). The systematic significance of these peculiarities may, to the fullest degree, be understood only with revision of all species (V.H.).

Geographic Distribution

Forested regions of middle and southern parts of East Asia, the Himalayas, Afghanistan and Baluchistan.

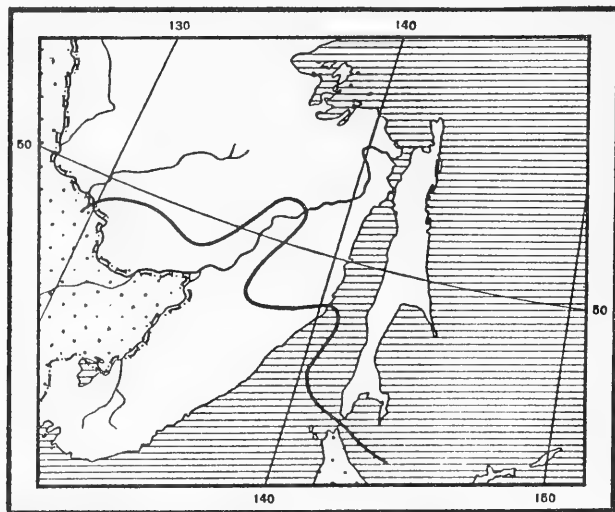


Fig. 174. Reconstructed northern limit of occurrence of white-chested (black) bear *Ursus (Selenarctos) thibetanus* G. Cuv. in USSR (V.G. Heptner).

Geographic Range in the Soviet Union

The range in the USSR comprises the extreme northeastern part of the species range and occupies a very small part of the country—Ussuri territory and the region adjacent to the Amur river on the north.

The northern border of the range runs from Innokenti Bay on the coast of the Sea of Japan (about 50 km south of Sovietsk Gavan) southwest to the region of chief heights (crest) of the Sikhote-Alin', crossing it at the sources of the Samarga. From this place, the boundary directs itself to the north, through the middle course of the Khor, Anyui and Khungari rivers and comes to the shore of the Amur, crossing it at the level of the Gorin r[iver] mouth. Along this river [Amur], the bear has been noted as far as 51° N. Lat. (Bagetor camp near Lake Evoron; K.A. Vorob'ev).

Thence, the boundary runs at some distance from the Amur valley along its left bank, being directed towards the southwest, and passes to the north of Lake Bolon' and the point of juncture of the Kur and Tunguska. The white-chested bear is encountered in the lower course of Urmi. Farther to the west, it occurs north of the bend of the Amur, between the mouth of Ussuri and 130°30' E. Long. and the Tyrma river on the north, and particularly on the southern slopes of Dur and Shuki-Pokta ranges. Thence, the boundary of the range, crossing the southern spurs of the Bureinsk
484 mountains—the Vand and Aagar-Aul ranges—exits into northeastern China along the southern slopes of the Malyi Khingan [range]. Probably, in some places, the bear penetrates somewhat farther north than the above-mentioned line. It is absent on Sakhalin.⁴⁹

In Ussuri territory, the black bear is not found everywhere, being restricted to the broad-leaved forests which are connected with the forests of the so-called Manchurian type; it avoids the open areas and the high parts of Sikhote-Alin'

⁴⁹The assertion of Sowerby (1923), concerning the occurrence of this species in Kamchatka, used by several authors, is without any foundation. Range according to Shrenk, 1858; Maak, 1861; Radde, 1862; Emel'yanov, 1927; Ognev, 1931; the data of K.A. Vorob'ev and, primarily, according to Bromlei, 1956.

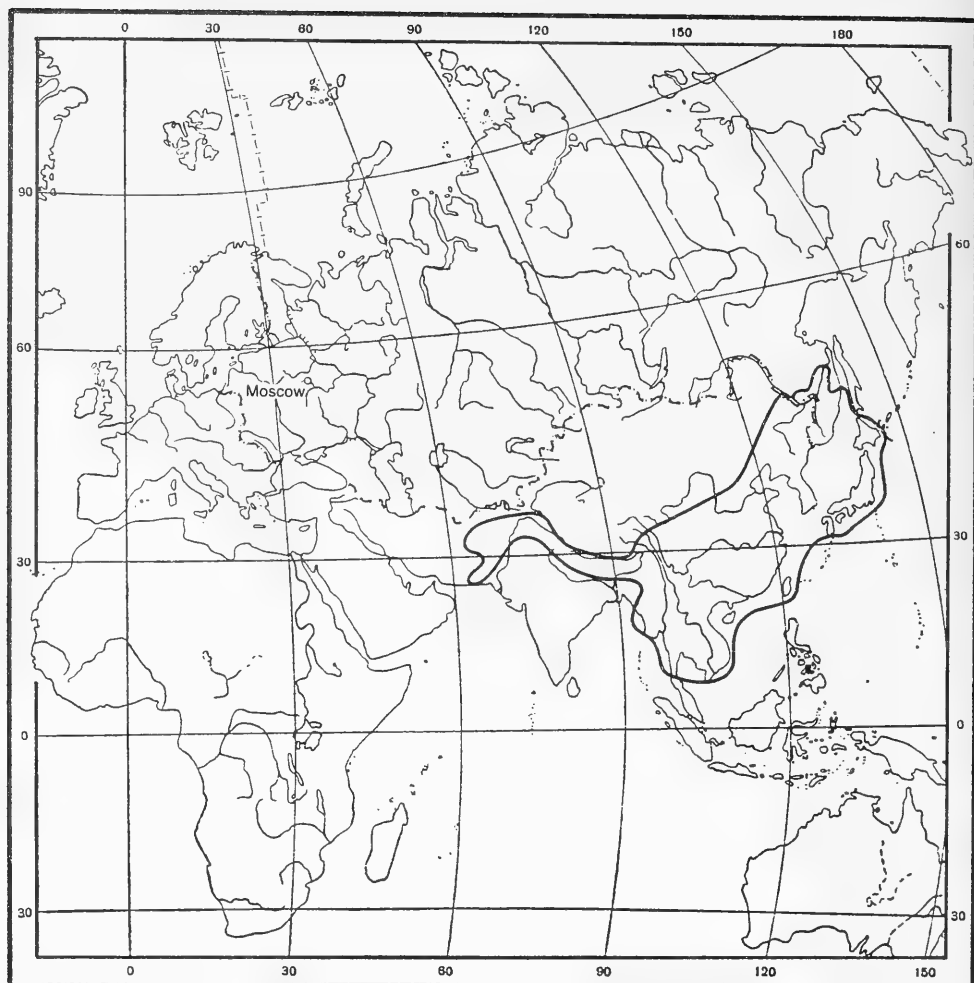


Fig. 175. Species range of the white-chested bear, *Ursus* (*Selenarctos*) *thibetanus* G. Cuv. (reconstructed) (V.G. Heptner).

Geographic Range outside the Soviet Union

The (reconstructed) range outside the USSR occupies Baluchistan (Suleiman mountains, but also Makran coast), the Hindu Kush [mountain] system (southern) in Afghanistan (D. Povol'nyi), Punjab, Kashmir, Himalayas within the boundaries of Nepal, Sikkim and Bhutan, and farther east—the southern slope, but locally, and apparently, also the northern side within the boundaries of Tibet. The

range includes Assam, Burma, Indochina Peninsula, Malay* Peninsula south to Mergui (12°30' N. Lat.) or to the northern boundary of the southern part of the Malay* Peninsula (about 7–7°30' N. Lat.), southeastern and eastern China, including Sichuan and Gansu, the eastern part of northeastern China, Hainan, Taiwan and the Japanese Islands (absent on Ryukyus).⁵⁰

At the present time, the range has changed considerably, except in the south and north, in the eastern half of China where the bear is absent; it exterminated in a series of places, and also in Japan (V.H.).

Geographic Variation

The described species has been given about 15 names. In the past, 7–8 races usually have been accepted, but this is, apparently, too many, especially if the small range of the species is considered. Some races were evidently described without sufficient basis. However, several are, apparently, well characterized. It is necessary to revise geographic variation in the species.

There is one subspecies within the boundaries of our country: Ussuri white-chested bear, *U. (S.) t. ussuricus* Heude, 1901. For description, see above.

Found in Ussuri and Amur territories.

Outside USSR—in northeastern China (former Manchuria), Korean Peninsula, and northern parts of eastern China.

The Ussuri bear is a well-defined form, distinguished from southern [forms], not to mention the insular ones, by its pure black, dense and long fur, and larger dimensions. For Kashmir bears, it is true, lengths of up to 202 cm and weight up to 181 kg have been recorded; however, the accuracy of these measurements is doubtful. In any event, animals with greatest length of skull more than 306 mm are not known from India, Pakistan, and Burma (Pocock, 1941). Therefore, the largest greatest length of skull of an Indian specimen is less than the average for this measurement in Ussuri bears. The largest recorded condylobasal length of skull of animals

*Russian original erroneously reads “Malakka”—Sci. Ed.

⁵⁰Older authors refer to its occurrence the entire archipelago (Temminck, 1847), and more recent (Ellerman and Morrison-Scott, 1951), only in Honshu (Hondo), Kyushu and (?) Shikoku.

from Hubei and Sichuan (275.0 mm; Allen, 1938), are also less than the average of our bears.

Outside the borders of our country, the following forms are usually accepted: 1) *U. (S.) t. gedrosianus* Blanf. 1877—Baluchistan; 2) *U. (S.) t. laniger* Pocock, 1932—Kashmir, Punjab, Afghanistan; 3) *U. (S.) t. thibetanus* Cuvier, 1823—from Nepal through Assam to Burma, Siam and Vietnam inclusive; 4) *U. (S.) t. melli* Matschie, 1922—from Yunnan to Fujian, Hainan; 5) *U. (S.) t. mupinensis* Heude, 1901—Sichuan, Shanxi, Hubei; 6) *U. (S.) t. japonicus* Schlegel, 1857— islands of Honshu (Hondo), Kyushu (?), Shikoku; 7) *U. (S.) t. formosanus* Swinhoe, 1864—Taiwan.

The small form, *japonicus* is very well-marked; the skull of a 2.5 year old female from Japan (Zoological Museum, Moscow University) has a greatest overall length of 226 mm, condylobasal length—198 mm, and zygomatic width—141 mm. As mentioned, *ussuricus* differs, apparently, from the well-validated insular form, *formosanus*, and the extreme southwestern form, *gedrosianus*. Distinctiveness of *laniger* from *thibetanus* and the validity of *mupinensis* are highly doubtful (V.H.).

Biology

Population. There are no accurate data on numbers. It is more numerous in southern Primor'e, and is rarely met with in the northern spurs of Sikhote-Alin' range. Within the limits of the Tachin-Chtan range, for each 20 white-chested bears, one brown bear is found. 486 In Sikhote-Alin' preserve, for one white-chested bear, 20 brown bears are found (Bromlei, 1956; Yu.A. Salmin and V.D. Shamykin).

Habitat. The white-chested bear prefers oak-broad-leaved and nut-pine-broad-leaved forests of the Manchurian type, and rarely occupies fir-spruce taiga and high-montane birch krummholz and montane balds. They avoid forests of the Okhotsk type.

They are more often encountered in river valleys and adjacent slopes.

They set off to the mountain tops only when there are crops of "nutlets" of nut-pines and red billberries.

Food. In April and May, before the appearance of green vegetation, the white-chested bear feeds at the expense of nut-pine "nutlets" and acorns of the previous year. In case of crop failure,



Fig. 176. Broad-leaved and coniferous broad-leaved forests of "Kedrovaya Pad'" preserve (southern Primor'e). Typical place of habitation of white-chested bear; here also are spotted deer, roedeer, wild bear, yellow-throated marten, leopard. June, 1963. Photograph by A.G. Pankrat'ev.

it searches in river valleys for nuts of Manchurian filbert [hazelnut], and captures insect larvae in rotten logs. Nursing females do not go far from dens, feeding also on young sedge and birch sap; the latter, possibly, favors removal of the "plug" from the rectum.

From mid-May and in all of June, food is monotonous—stems of coltsfoot, cow parsnip, angelica, sedge, ovaries of oak, leaves of Amur cork tree and Manchurian walnut; from the end of June, they add the fruits of honeysuckle, searching in old burns along sunny slopes.

All of July, August and part of September, its main food consists of fruits of bird-cherry which the bears eat while climbing trees. While eating, they bend and break branches beneath themselves, as a result of which places are formed in crotches of trunks—"nests"; such "nests" also originate in oaks with feeding



487 Fig. 177. Black-fir-hornbeam forest in "Kedrovaya Pad'" preserve—biotope of white-chested bear. Southern Primor'e. 20 September 1964. Photograph by A.G. Pankrat'ev.

by bears on acorns. In August, food also includes Amur jack-in-the-pulpit and its bulbs, iris, ovaries of oak and other plants.

488 In September, to bird-cherry they add acorns (often still unripe), nut-pine cones, actinidia vine, Amur grape and rarely, still-green filbert nuts; green plants disappear from the diet. At the end of September, nut-pine "nutlets" and acorns become the principal food and remain so in harvest years until retirement to the den.

In years of crop failure, white-chested bears descend to river valleys and springs and, before retiring into dens feed on Manchurian walnuts, Amur grapes, actinidia and rarely on berries of Amur cork tree. Under these conditions, they almost never climb trees. Predatoriness is not typical for the white-chested bear, even with no crops of their principal foods. In rare cases, bears feed on carrion and fish which die after spawning (*sima* salmon) [*O. masu*] but, as a rule, they do not eat fish.



487 Fig. 178. Burrow of a hibernating Siberian chipmunk destroyed by white-chested bear with goal of taking store of nut-pine "nutlets". "Kedrovaya Pad'" preserve. 5 November 1964. Photograph by A.G. Pankrat'ev.

Home range. There is no information. In spring, the nursing females do not move farther than 1–1.5 km from the den.

Burrows and shelters. In winter, the white-chested bears retire to hollows in old trees, usually Maximovich poplar, and *Chosenia*, linden and oak. They also frequently hibernate in caves and rocks. If disturbed, or driven from dens, they occasionally lie down in hollows without shelter, on the ground at the base of a tree, and beneath roots.

Of 42 dens, 55% were situated in hollow [trees] (linden—22%, poplar—26%, oak—7%), in rocks—38%, and directly on the ground—7% (Bromlei, 1956). The percentage of dens in rocks is, apparently, inflated, because they are easily discovered. Bears occupy dens for many years in a row. Animals grossly fattened—bears well fed for winter—may not be able to pass through entrances of hollows, and therefore, large bears more often retire in rocks in [good] food years.



488 Fig. 179. Hollow in Amur linden, in which there were wild Indian bees torn apart by white-chested bear to obtain honey. "Kedrovaya Pad' " preserve, Southern Primor'e. November 1962. Photograph by A.G. Pankrat'ev.

Daily activity and behavior. The daily cycle of activity is not known. Behavior of the white-chested bear differs from the brown in that it often climbs trees and feeds on them. They also climb in thickets of vines.

Hibernation and winter sleep. In autumn, the white-chested bears accumulate fat more quickly and simultaneously than brown, and retire to dens somewhat earlier (V.D. Shamykin, Yu.A. Salmin). With the onset of cold, these bears are rarely met with, and at the end of October–beginning of November, even before snowfall, they have disappeared. Cases of delay in retirement and arousal

489 (“shatun”) have not been noted in this species (Sikhote-Alin’ range). However, in Tachin-Chtan range, white-chested bears retire later than brown (Bromlei, 1956). Individual animals were seen in the marine littoral zone at the end of December. At the beginning of winter, they sleep lightly, later on—heavily. Females with cubs do not leave the hollows even when smoked. Exit from the den in spring occurs later than in the brown—in the second half of April, when the snow has already melted. Therefore, white-chested bears do not experience sharp spring hunger. Near the sea and on the southeastern slopes of the Sikhote-Alin’, bears wake up earlier than in the interior of the mainland; those lying in hollows exit later than those lying in rocks; females with cubs get up last of all up. Sometimes, after a heavy late snowfall in April, they again retire. Animals driven from dens sometimes go to sleep again—even in the open at the base of a tree trunk; cases are known when a female bear in such a position carried the cubs and hid them in her abdominal wool (Bromlei, 1956). In the den, they thin little during the period of winter sleep, and only the nursing females lose fat; fat is primarily consumed in the period of spring food shortage.

Seasonal migrations and transgressions. In searching for food, bears undertake movements of about 200–350 km. They occur more frequently than in the brown bear, but for lesser distances, and they are closely connected with yield and distribution of the main plant foods (nuts, acorns).

Reproduction. In Sikhote-Alin’, rut in the white-chested bear is initiated earlier than in the brown—from the middle of June to the middle of August. Accordingly, birth takes place earlier: nursing females were taken from the middle of January (Yu.A. Salmin, and V.D. Shamykin). Mating was noticed in the region of the Tachin-Chtan range from the first days of June to the end of July (wide paths, flattened areas of trampled grasses with 10–15 m diameter). The first signs of pregnancy (swelling of uterine horns to 15–22 mm) are observed in October. By the end of December, the weight of the embryo reaches 75 g. All dates of reproduction have an amplitude [of variation] of 2 months (Bromlei, 1956). Barrenness is a frequent phenomenon (for 1 pregnant female—2 barren).

The female gives birth to 2 offspring, rarely 3, beginning from the end of December (very rarely) to the middle of February, occasionally to the beginning of March, but most often from the middle of January to the middle of February.



Fig. 180. Hollow of wild Indian bees in Daurian birch, torn apart by white-chested bear. "Kedrovaya Pad' " preserve, southern Primor'e. March 1965. Photograph by A.G. Pankrat'ev.

490 *Growth, development, and molt.* The bear-cubs are born blind, weighing 300–450 g, and differ from the brown in the greater length of their feet and claws. They grow slowly, reaching in May only 2.5 kg (rarely 4.0 kg). Sometimes, "runts" occur, weighing at the end of summer 6–7 kg (diseased or born late). The first month after her departure from the den, the she-bear boldly defends the cubs (April–first half of May). In June, after driving the cubs into trees, she flees (Bromlei, 1956).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Tigers and wolves may be enemies of the



Fig. 181. Clearing with tall grasses in the forest of "Kedrovaya Pad' " preserve, southern Primor'e. Place of feeding of white-chested she-bear with cubs. August 1963. Photograph by A.G. Pankrat'ev.

white-chested bear, and for cubs, also lynx. The tiger can cope with a bear weighing 60 kg.

The white-chested bear rarely comes across the brown, because they primarily restrict themselves to different altitudes and occupy different stand-types. They are found frequently together only in certain stand-types (foothills, seashore) in years of acorn harvest.

In April (mainly), they are attacked by ticks; in August, lice are observed. Infestation with intestinal worms is negligible (Bromlei, 1956).

The frequency of occurrence of the white-chested bear in the region of the Tachin-Chtan range is not constant; changes are directly related to the autumn food crop (nuts, acorns). In 1944 in this region, following a doubling of the yield of acorns and nut-pine "nutlets", a considerable concentration of bears emerged.

Field characteristics. Signs of activity of the white-chested bear differ from those of the brown in the presence of "arbors" of twigs in the forks of trees, and in claw marks on the bark [of trees] to a height of more than 2.5 m.* Animals frequently climb in thickets of vines, and dig a lot in the ground (P.Yu.).



491 Fig. 182. "Nest" made of broken branches left in the tree top after feeding by white-chested bear on the fruits of a large tara vine (actinidia). "Kedrovaya Pad'" preserve, southern Primor'e. September, 1958. Photograph by A.G. Pankrat'ev.

*Lapsus ? Brown bears are more likely to leave claw marks at a height of "more than 2.5 m. than are the much smaller white-chested bear—Sci. Ed.

Practical Significance

The white-chested bear yields skin, meat and fat of greater value than does the brown bear. It does not belong among the predators injurious to game or domestic animals. Dens of the white-chested bear are easily discovered, and therefore the animal is easily exterminated; it is in need of protection. Its utilization must be strictly



Fig. 183. Marks of an Asian black bear on a white-barked fir. Marks made in spring. Western shore of Amur Gulf, southern Primor'e. June, 1962.

Photograph by A.G. Pankrat'ev.

regulated. In the case of den-hunting, tree hollows are often destroyed, which reduces the number of shelters necessary for overwintering.

They are hunted with dogs (P.Yu.).



MAMMALS OF THE SOVIET UNION

Volume II, Part 2

This volume, is part of a three-volume monograph, and is a continuation, of Volume II, Part 1, which was devoted to sea cows and carnivores. It contains species descriptions of terrestrial carnivores and detailed information on their external morphology, skull, body measurements and other data, affinities with other species, geographic distribution in the historic past and today, geographic variation, practical significance, and biology. Descriptions are presented for orders, families, and genera, and keys given for their identification.

The book is richly illustrated with photographs, sketches, and colored illustrations by the famous wild life painter, A.N. Komarov, and the zoologist-artist, N.N. Kondakov.

The results of original scientific studies are published here for the first time, providing readers a vast wealth of material heretofore unknown. This work is intended for teachers and students of faculties of biology and geography in universities, as well as pedagogic, agricultural, and forest institutes, similar organizations, workers engaged in game, fur, forest and fish trades; those interested in the conservation of nature, and all persons interested in zoology and nature study.

MAMMALS OF THE SOVIET UNION

Volume II, Part 3

This volume is fourth book of *Mammals of the Soviet Union*, representing the third part of the second volume; it is devoted to descriptions of the orders of Soviet aquatic mammals — pinnipeds (Pinnipedia) and, in part, cetaceans (Cetacea), toothed whales (Odontoceti). In the sequence of descriptions from the "higher" to the "lower" orders adopted in this series, pinnipeds should have preceded carnivores, i.e., should have appeared in the second book. The grouping of the orders at a higher level is given after G.G. Simpson (1945). The sequence of genera and species within the orders has been retained as before, i.e., from the less specialized to the more specialized.

The order of pinnipeds or seals (Pinnipedia) is described in this volume. The cohort of ungulates and carnivores represented in Soviet fauna by orders of artiodactyls, and perissodactyls, sirenians, carnivores, and pinnipeds thus came to an end and the cohort of whales (Mutica) commences. The toothed whales are described in this volume.

While it has not always been possible to maintain a totally uniform description of the genera and species as in the volumes already published, in spite of every effort to do so, the sequence has been adhered to, with some exceptions, in the case of Pinnipedia. But, it was impossible to use same format in describing the toothed whales (Odontoceti). Only a brief morphological description has been given for many species, which is more or less adequate for identifying the species. General information on their distribution and fragmentary biological data are also given. In some cases the total absence of such information is indicated.